VOL. XI APRIL 1957 NO. 2

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

IN THIS ISSUE: Dumbleton — *New Zealand Aleyrodidae* • Wilson — *Taxonomy of the Genus* Eugenia *in Hawaii* • Palmer — *Origin and Diffusion of the Herzberg Principle* • Banner — *Alpheid Shrimp of Arno Atoll* • Carlquist — *Systematic Anatomy of* Hesperomannia • Reish — *Life History of* Neanthes caudata • Boden and Kampa — *Records of Bioluminescence in the Ocean* • de Laubenfels — *New Species and Records of Hawaiian Sponges*

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(Continued on inside back cover)

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The New Zealand Aleyrodidae (Hemiptera: Homoptera)[1]

L. J. DUMBLETON[2]

THE PIONEER WORKER on the New Zealand Aleyrodidae was W. M. Maskell, who also described species from all over the world. The Maskell collection of Aleyrodidae is therefore an important one. It has recently been returned to New Zealand after having been on loan to the Bureau of Entomology of the United States Department of Agriculture for many years and is now, together with the equally important Maskell collection of Coccidae, in the collection of the Entomological Research Station of the Department of Scientific and Industrial Research at Nelson.

It is desirable that Maskell's species should be redescribed. This task has been facilitated by the location of Maskell's unmounted duplicate material of some species and the collection of others from the field. In addition to Maskell's species there is one New Zealand species described by Takahashi (1937). Two species are described as new.

Considerable confusion has centered around Maskell's genus *Asterochiton*, though this has been clarified, in so far as it affects the genus *Trialeurodes*, by Russell (1948).

Maskell (1879) described the first Aleyrodids from New Zealand. These were *lecanioides* (which has page precedence) and *aureus*, for which two species he created a new genus *Asterochiton*, placing it in error as a Coccid genus. No genotype was designated and it is doubtful if his definition of the genus, "characterised by enclosure in a test," is an adequate generic prescription. The figure and description of *aureus* is quite recognisable, while that of *lecanioides* suggests *Trialeurodes vaporariorum* Westw. Maskell (1880) recognised his error and removed his two species of *Asterochiton* from the Coccidae to the Aleyrodidae. In 1890 (pp. 175–176) he repeats the correction and, apparently considering that the genus *Asterochiton* was invalidated or unnecessary, discontinued its use in favour of *Aleurodes*. The species *lecanioides* he stated to have been based on material containing two species, which he now described as *Aleyrodes papillifer* and *A. simplex*. The name *lecanioides* should have remained valid in reference to the *vaporariorum*-like species which he first described. Apparently considering that the invalidation of the genus *Asterochiton* also invalidated the species *aureus* he discarded this name and redescribed and named the same species as *Aleurodes melicyti*. In the same year he described *Aleurodes asplenii* and *A. fagi*. In 1896 he described *A. cerata* and *A. fodiens*.

Cockerell (1902) listed Maskell's species and stated that *papillifer* was a synonym of *lecanioides* and *melicyti* was a synonym of *aureus*. He revived Maskell's name *Asterochiton* as a subgenus of *Aleyrodes*, defined the subgenus, and cited *aureus* as the genotype. He also stated that *lecanioides* did not belong to the subgenus *Asterochiton* as defined by him. He defined the subgenus *Trialeurodes* and nominated *pergandei* Quaintance as the genotype.

[1] Work performed, in part, while a member of the Entomological Research Station, D.S.I.R., Nelson. Manuscript received February 8, 1956.

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Kirkaldy (1907) gave *Asterochiton* Maskell as a subgenus of *Aleyrodes* and cited *lecanioides* as genotype, stating that Cockerell was wrong in citing *aureus* as genotype.

Quaintance (1908) gave *Asterochiton* Cockerell as a subgenus of *Aleyrodes*, with *aureus* Maskell as genotype, and listed *melicyti* Maskell as a synonym of *aureus* and *papillifer* Maskell as a synonym of *lecanioides* Maskell.

Quaintance and Baker, who published three papers on the classification of the Aleyrodidae, had Maskell's type material available for study. In the 1914 paper (p. 109) *vaporariorum* Westw., of which *lecanioides* Mask. and *papillifer* Mask. are listed as synonyms, is given as the genotype of *Asterochiton* Maskell because these authors wrongly believed Maskell to have designated *lecanioides* as the genotype of *Asterochiton* and, on examination of the type of *papillifer*, found it to be a synonym of *vaporariorum* Westw. Quaintance and Baker (1914: 98), overlooking the fact that Cockerell had designated *aureus* as the genotype of *Asterochiton*, erected a new genus *Dialeurodoides* with *aureus*, which they figured, as genotype, and included in it *fagi* Mask. and *simplex* Mask. In a correction (1915: xi) it was stated that *Asterochiton* of the 1914 paper must replace *Dialeurodoides* Q. and B., and that *Trialeurodes* Cockerell must replace *Asterochiton*. Cockerell's designation of genotypes has priority over those of Kirkaldy (1907) and Quaintance and Baker (1914) and the species congeneric with *aureus* belong to *Asterochiton* Maskell and those congeneric with *pergandei* belong to *Trialeurodes* Cockerell. Quaintance and Baker in the 1914 paper, as amended by the 1915 correction, placed *fodiens* Mask. in *Dialeurodes* and *asplenii* Mask. in *Trialeurodes*. Quaintance and Baker (1917) redescribed and figured *Dialeurodes fodiens* Mask.

Takahashi (1937) described and figured *Aleyrodes winterae*.

The New Zealand Aleyrodid fauna, as it is known at present, is a limited and fairly homogenous one in which only the subfamily Aleyrodinae is represented. The subfamily Udamoselinae is represented in Australia, and Maskell described a species of *Aleurodicus* from Fiji, though it is possibly introduced. The New Zealand fauna shows no obvious affinities with the much larger and more generically diversified fauna of Australia, with that of New Caledonia, or with the limited faunas described from Chile and the insular Pacific region.

Subfamily *ALEYRODINAE* Enderlein

GENERIC KEY TO PUPAL CASES OF NEW ZEALAND SPECIES

1. Numerous papillae in single row on submargin, lingula knobbed and lobed . . . . . **Trialeurodes** Cockerell

   Not as above 2

2. Thoracic and abdominal pore areas invaginated, tracheal comb teeth present . . . . . **Asterochiton** Maskell

   Not as above 3

3. With marginal or submarginal setae, caudal furrow absent . . . . **Aleyrodes** Latreille

   Not as above . . . . . **Aleuroclava** Singh

KEY TO ADULTS OF NEW ZEALAND SPECIES OF *Aleyrodidae*

1. Antenna with segment 7 twice as long as 6; hind tibiae with comb of 30–34 setae; forewing 1.8 mm. long, R_1 present; lingula widest at apex, truncate, with 4 conical processes . **Asterochiton aureus** Maskell

   Antennal segment 7 not twice as long as 6; hind tibia with not more than 22 setae in comb; wing not longer than 1.5 mm. without R_1 or with stub only; lingula if truncate without apical processes and widest before apex 2

2. Penis in lateral view subparallel sided . . 3

   Penis tapering 6

3. Penis narrow, strongly sinuate, apex truncate; wing with stub of R_1 present; lingula truncate, excised at corners of apex . . . . . **Aleuroclava eucalypti** n. sp.
   Penis wide, not sinuate, apex toothed; lingula rounded apically 4
4. Apical tooth of penis longer, more pointed; antennal segment 5 nearly twice as long as 6 . . . . . **Aleyrodes fodiens** Maskell
   Apical tooth of penis shorter, more rounded; antennal segment 5 slightly longer than 6 5
5. Apex of penis narrowed abruptly at nearly right angles, to base of apical tooth . . . . . **Asterochiton pittospori** n. sp.
   Apex of penis narrowed obliquely at 45 degrees, to base of tooth . . . . . **Asterochiton simplex** (Maskell)
6. Penis more strongly hooked or falcate apically; antennal segment 3 longer than 4–6 combined; wing length 1.5 mm.; lingula truncate apically . . . . . **Trialeurodes asplenii** (Maskell)
   Penis apex less strongly hooked; antennal segment 3 shorter than 4–6 combined; wing length 1.0 mm.; lingula truncate-excavate apically . . . . . **Trialeurodes vaporariorum** (Westw.)

Genus TRIALEURODES Cockerell

KEY TO PUPAL CASES OF NEW ZEALAND SPECIES OF *Trialeurodes*

With up to 7 larger, circular papillae on the submargin in addition to the more numerous smaller conical papillae; unpigmented in median areas . . . . . **vaporariorum** (Westw.)
Submarginal papillae uniform in size; pigmented on cephalic and abdominal median areas . . . . . **asplenii** (Maskell)

Trialeurodes asplenii (Maskell)
Figs. 1, 2

Aleurodes asplenii Maskell 1890: 173–4, pl. 13, figs. 18–20.

Aleyrodes asplenii Maskell. Cockerell, 1902: 281; Kirkaldy, 1907: 46; Quaintance, 1908: 5.

Asterochiton asplenii (Mask.) Quaintance and Baker, 1914: 105, and footnote p. 104.

Trialeurodes asplenii (Mask.) Quaintance and Baker, 1915: xi.

LARVA: Described by Maskell (1890: 174, fig. 18). Specimen not located.

PUPAL CASE: (Fig. 1). Length 1.0 mm., width 0.7 mm. Derm pale but with light brown pigmentation in the median cephalic area and in the median and subdorsal area of abdominal segments 2–6 inclusive. Elliptical, widest behind mid-length, raised on vertical white wax palisade. Margin crenulated, about 20 crenulations in 0.1 mm. Thoracic tracheal fold present. Tracheal pore (Fig. 2*a*) semicircular, with 4–5 marginal crenulations opposite the pore narrower than the others. Abdominal tracheal fold and pore absent, crenulations not noticeably narrower. Submarginal area with a single row of about 55 fairly sharply conical papillae of uniform size on each side. Abdominal segment 7 not as narrow as in *vaporariorum*. Subdorsal papillae absent. One pair of para-median cephalic setae, one pair on each of first and 8th abdominal segments and one pair of caudal setae (Fig. 2*b*). Posterior marginal setae present. Vasiform orifice (Fig. 2*c*) subcordate, notched posteriorly, length 0.085 mm., width 0.06 mm. Operculum occupying about half the orifice, length 0.04 mm., width 0.05 mm. Lingula clubbed, with three paired lateral lobes and one unpaired median caudal lobe and two apical setae. Caudal furrow absent.

ADULT: (Fig. 2*d*, *e*). *Female*, antennae with segment 3 longer than segments 4–6 combined, segments 4 and 6 subequal and shorter than 5 and 7, 5 longer than 7, flagellum of 7 much shorter than base. Wings white, immaculate, forewing length 1.5 mm. Hind tibia with about 16 setae in comb. *Male*, operculum (Fig. 2*d*) transverse, 0.02 mm. long, 0.04 mm. wide, posterior margin concave. Lingula

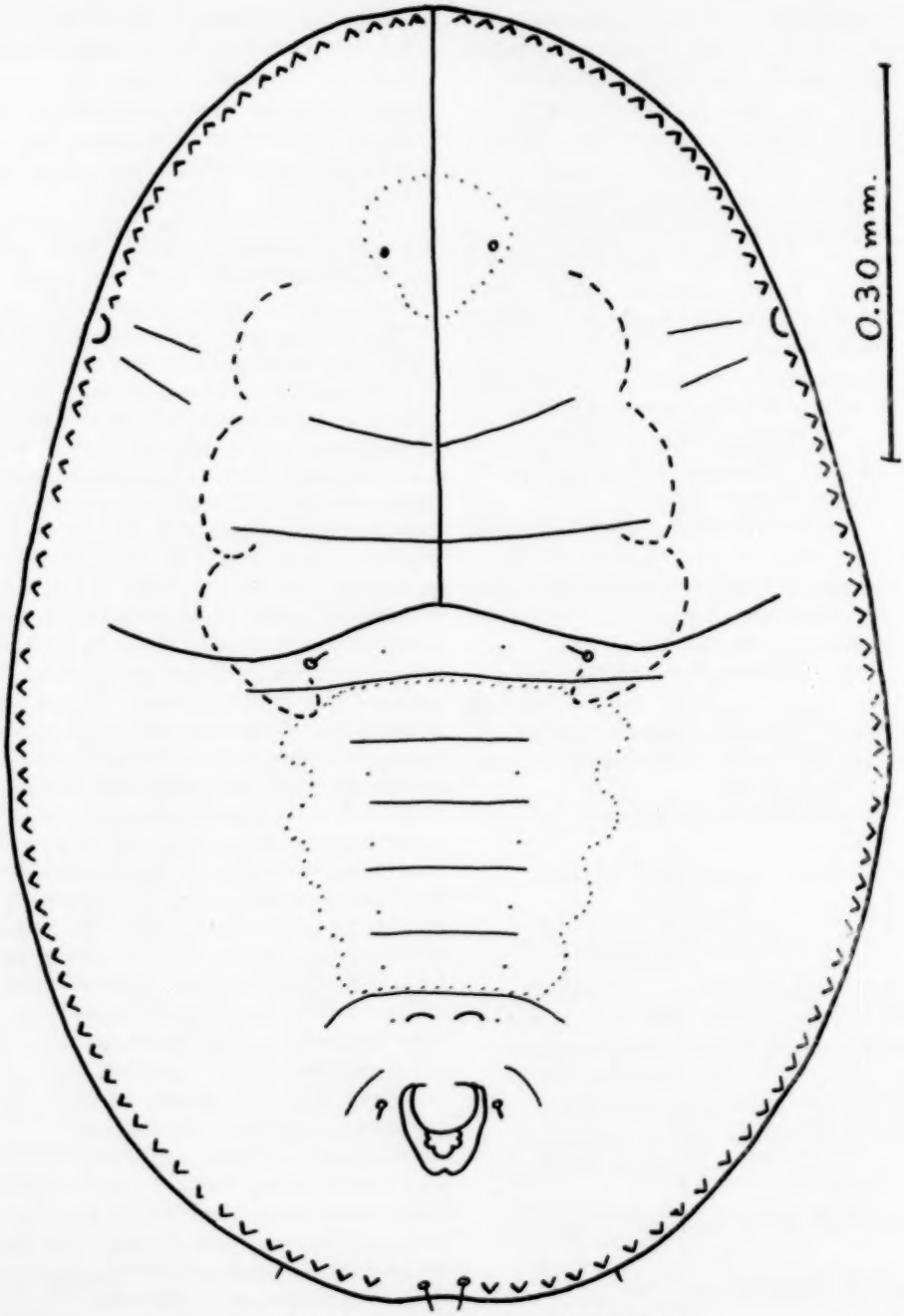


FIG. 1. *Trialeurodes asplenii* Mask. Pupal case, dorsal.

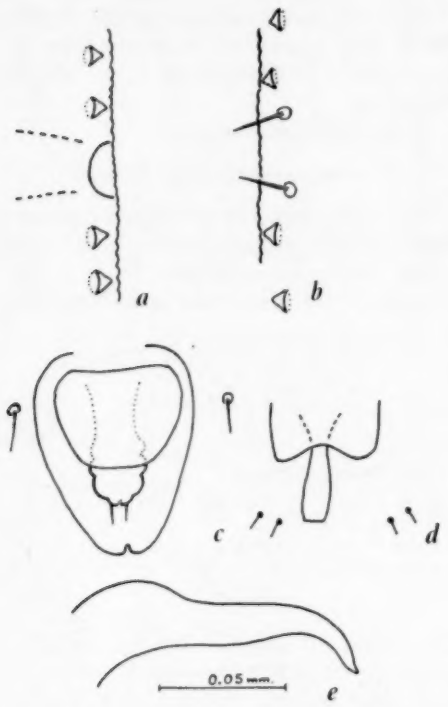


FIG. 2. *Trialeurodes asplenii* Mask. Pupal case: *a*, Thoracic tracheal fold and pore; *b*, caudal margin; *c*, vasiform orifice. Adult male: *d*, Operculum and lingula; *e*, penis, lateral view.

about 0.04 mm. long, 0.01 mm. wide, constricted near base, truncate apically. Penis (Fig. 2*e*) tapered to apex which is pointed not truncate and curved dorsally. Slightly sinuate above and below, length 0.11 mm.

LECTOTYPE: Pupal case on slide mount. Maskell collection.

TYPE LOCALITY: New Zealand.

FOOD PLANT: Fern, *Asplenium lucidum* and other ferns.

COTYPE: Pupal case on slide mount, U. S. Bureau of Entomology.

OTHER MATERIAL: Slide mounts of genitalia and wings and unmounted duplicate material in Maskell collection. Unmounted duplicate material (3 pupae and one larva) in U. S. Bureau of Entomology. Pupal cases and adults from *Asplenium lucidum*, Ruby Bay, Nelson, Jan. 1952, in the author's collection.

There are no undoubtedly endemic species of *Trialeurodes* known in Australia or New Zealand and since *asplenii* occurs on *Asplenium* and other ferns it could well have been introduced on ornamental ferns and not be native to New Zealand.

Trialeurodes vaporariorum (Westwood)
Figs. 3–5

Aleyrodes vaporariorum Westw. 1856. Gardeners Chronicle, p. 852.

Asterochiton lecanioides Maskell, 1879: 215–216 (in part), 1880: 300–301 (in part); Quaintance and Baker, 1914: 105.

Aleyrodes lecanioides (Mask.). Cockerell, 1902: 281; Kirkaldy, 1907: 60.

Aleurodes papillifer Maskell, 1890: 173, 1896: 438.

Asterochiton papillifer (Mask.). Quaintance and Baker, 1914: 105.

Trialeurodes lecanioides (Mask.). Quaintance and Baker, 1915: 11; Russell, 1948: 7–8, 43–45.

Trialeurodes papillifer (Mask.). Quaintance and Baker, 1915: 11; Russell, 1948: 7–8, 43–45.

PUPAL CASE: (Fig. 3). Length 0.75–0.10 mm., width 0.5–0.75 mm. Derm thin and colourless except for the papillae. Shape elliptical. Case raised off leaf on vertical palisade of white wax. Margin (Fig. 4*a*) crenulated, about 12 crenulations in 0.1 mm. Thoracic tracheal pore area (Fig. 4*b*) marked by narrowing and depth of 3–10 crenulations. Commonly 75–110 submarginal papillae in a single row; 1–9 pairs may be larger than the others but these may be absent. Usually four pairs of subdorsal papillae but these may be absent. When present one pair is cephalic, one pair mesothoracic and one pair on each of the third and fourth abdominal segments. Setae; one pair cephalic, one pair first abdominal, one pair 8th abdominal often very long, and one pair caudal usually long. Vasi-

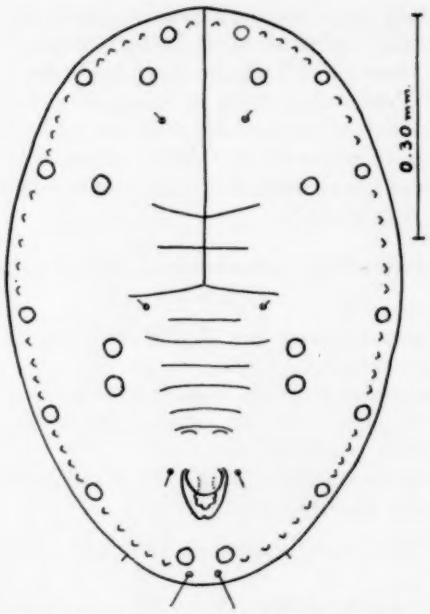


FIG. 3. *Trialeurodes vaporariorum* Westw. Pupal case, dorsal.

form orifice (Fig. 4*c*) 0.056–0.076 mm. long, 0.056–0.070 mm. wide, cordate, notched at posterior tip and with prominent tooth in notch. Operculum 0.036–0.048 mm. long and 0.044–0.060 mm. wide, cordate. Lingula 0.040–0.060 mm. long, 0.024–0.032 mm. wide, with two long setae and three pairs of lateral lobes and one median unpaired lobe. Caudal furrow present narrow.

ADULT: *Female*, antennae (Fig. 5*a*) with segment 3 shorter than segments 4–6 combined, 5 nearly twice as long as 6, flagellum of 7 short. Wings white unspotted, forewing 1.0 mm. long, R_1 absent. Hind tibiae with 13–16 setae in comb. *Male*, operculum (Fig. 5*b*) 0.02 mm. long, 0.045 mm. wide. Lingula truncate and excavate apically, length 0.03 mm., width 0.01 mm. Penis (Fig. 5*c*) length 0.1 mm., tapering and slightly falcate at apex in lateral view.

FOOD PLANTS: Recorded by Maskell from *Pittosporum eugenioides* and *Geniostoma* sp. Common on tomato and other plants.

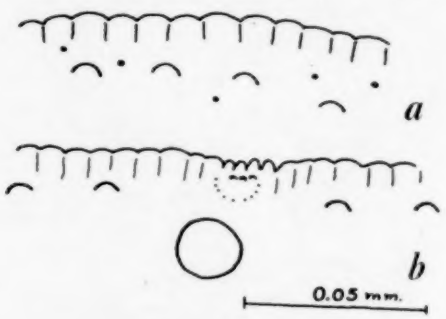
MATERIAL: A slide of *papillifer* (dated 1889, W. M. M.) stained and remounted by the U. S. Bureau of Entomology in the Maskell collection.

A cosmopolitan species.

Genus ASTEROCHITON Maskell

The generic prescription of Quaintance and Baker (1914: 98) and Sampson (1943: 208) must be amended as follows:

Medium in size, subelliptical to sub-



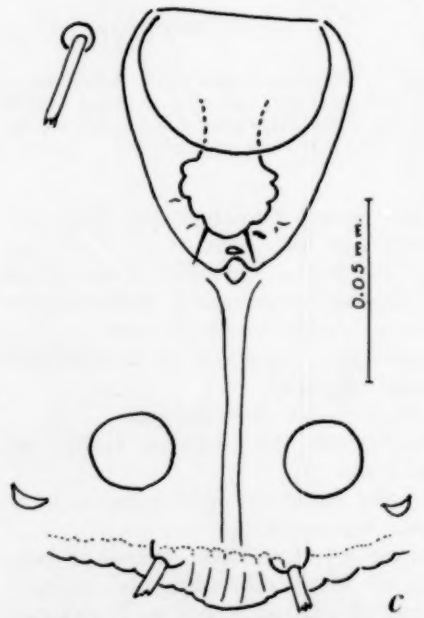


FIG. 4. *Trialeurodes vaporariorum* Westw. Pupal case: *a*, Margin; *b*, thoracic tracheal pore; *c*, vasiform orifice and caudal margin.

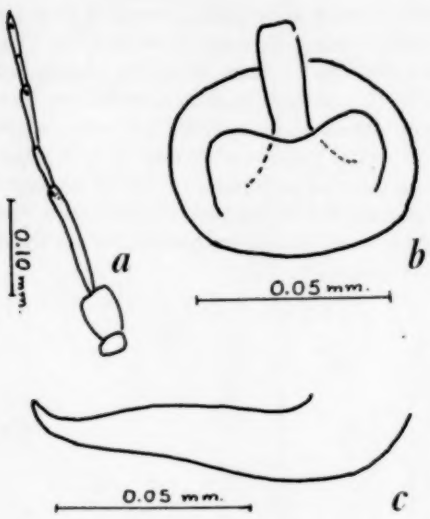


FIG. 5. *Trialeurodes vaporariorum* Westw. Adult female: *a*, Antenna. Adult male: *b*, Vasiform orifice; *c*, penis.

circular in shape. Margin with one row of teeth. Submargin may be separated from dorsal disc. Thoracic tracheal folds and combs present. Caudal fold may be indicated, comb present. Vasiform orifice subcordate, may be pointed posteriorly. Operculum transversely semicircular, subcordate or subtrapezoidal, filling about half the orifice. Lingula expanded at tip, bluntly pointed or rounded, exposed, included.

KEY TO PUPAL CASES OF NEW ZEALAND SPECIES OF *Asterochiton*

1. With four prominent radial pore bands on disc; pores present on submargin . . . . . **aureus** Maskell

   Not as above 2

2. With 13 prominent submarginal setae on each side . . . . . **fagi** (Maskell)

   Not as above 3

3. Without discal setae; submargin defined . . . . . **cerata** (Maskell)

   Not as above 4

4. Abdomen with 4 pairs of setae laterad on disc on segments 5–8 . **simplex** (Maskell)

   Abdomen with only one pair of setae laterad on disc, on segment 4 . . . . . **pittospori** n. sp.

Asterochiton aureus Maskell
Figs. 6–8

Asterochiton aureus Maskell. 1879: 216, pl. 7, fig. 17d; 1881: 301.
Aleurodes melicyti Maskell. 1890: 174, pl. 13, figs. 21–24.
Aleyrodes (*Asterochiton*) *aurea* (Mask.) Cockerell, 1902: 282.
Aleyrodes (*Asterochiton*) *aureus* (Mask.) Kirkaldy, 1907: 47; Quaintance, 1908: 5.
Dialeurodoides aureus (Mask.) Quaintance and Baker, 1914, pp. 98–99, pl. 37, figs. 7–11.
Asterochiton aureus (Mask.) Quaintance and Baker, 1915, p. xi; Sampson, 1943: 208; Russell, 1948: 7–8.

PUPAL CASE: (Fig. 6). Length 1.1 mm., width 1.0 mm. Colour golden yellow, pale brown in median area. Shape subcircular. Margin (Fig. 7*a*) irregularly toothed, about 10 teeth in 0.10 mm. The teeth do not appear to constitute the actual margin which is clear and straight. Thoracic tracheal fold (Fig. 7*b*) distinct, pore abruptly invaginated and with comb of 3–6 teeth. Abdominal tracheal pore (Fig. 7*c*) similar. Setae: posterior marginal, caudal and 8th abdominal setae present. Submarginal area 0.045 mm. wide with numerous large pores and separated by a line mesad of the pores from the dorsal disc. Similar pores are present on the anterior cephalic area of the disc before the cephalic ridge and a few on either side of the caudal furrow. On the disc are four radiating rows of similar pores, two immediately above the thoracic tracheal folds and two on the abdomen just caudad of the transverse moulting suture. The location of the smaller simple pores is shown in the figure. On the cephalic region are two paramedian transverse ridges on each of which are three or four simple pores. Above the

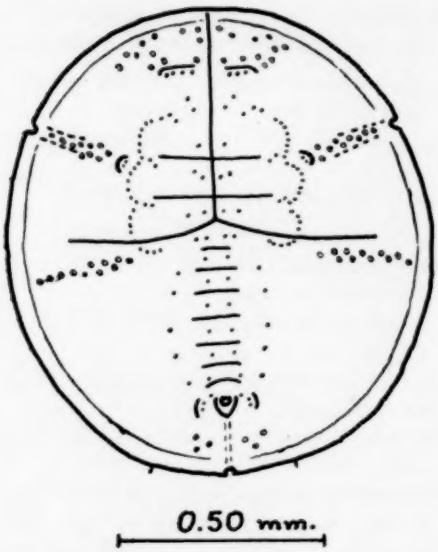


FIG. 6. *Asterochiton aureus* Mask. Pupal case, dorsal.

inner ends of the thoracic folds is a tubercle bearing 2 or 3 simple pores. The vasiform orifice (Fig. 7*c*) is subtriangular 0.06 mm. long and 0.057 mm. wide and acute posteriorly. Operculum is semicircular with a concave anterior margin, 0.04 mm. wide and 0.027 mm. long. The lingula is long; exposed apically and pointed but not acutely so. The floor of the orifice is reticulate. Neither the lingula nor the posterior apex of the orifice is as pointed as is figured by Quaintance and Baker (1914). Caudal furrow present, narrow.

Parasitised pupae are convex, with a narrow glassy white wax ring which is sloping and not vertical. There are white marks in this rim opposite the tracheal pores. The pupa is dark brown to black in the central disc with golden brown margins. There are strong radial ridges coinciding with the four radial pore bands and fainter ridges from each side of the cephalic ridge to the margin and from each side of the orifice to the margin.

ADULT: *Female*, antennae: segment 3, 0.23 mm.; 4, 0.06; 5, 0.07; 6, 0.05; 7, 0.11 mm. long; base of 7 is about ¾ the total length. Wings white immaculate, forewing (Fig. 8*a*) 1.8 mm. long, R_1 present. Hind tibiae (Fig. 8*b*) with 30–34 setae in comb. Operculum (Fig. 8*c*) excised posteriorly with two setae on posterior margin, width 0.04 mm., length 0.025 mm. Lingula widening to apex, truncate, lobed at each posterior lateral angle and with two conical processes between these with apical setae. Lingula length 0.035 mm., width 0.01 mm.

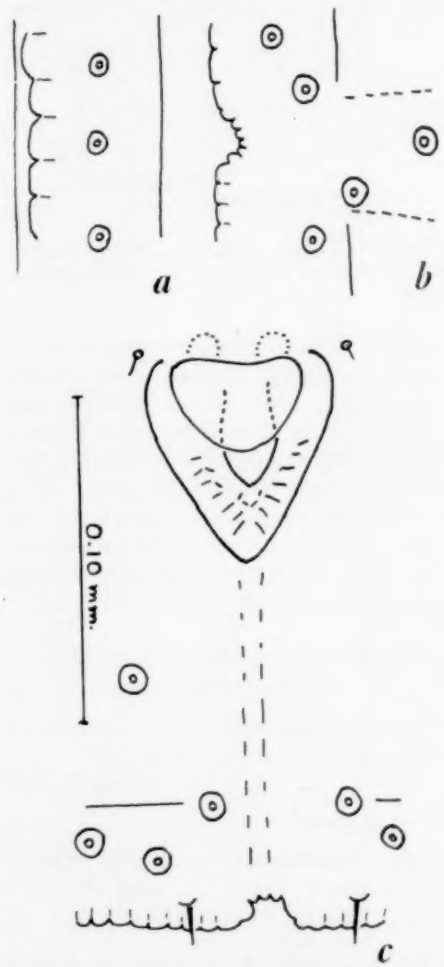


FIG. 7. *Asterochiton aureus* Mask. Pupal case: *a*, Margin; *b*, thoracic tracheal fold and pore; *c*, vasiform orifice and abdominal tracheal pore.

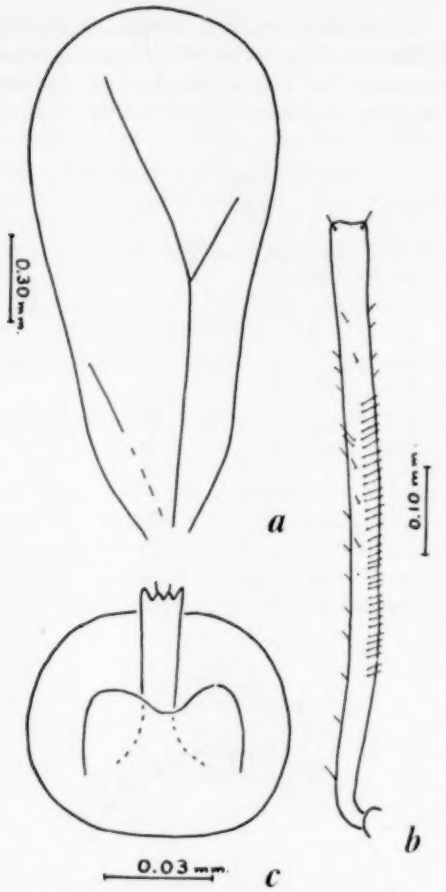


FIG. 8. *Asterochiton aureus* Mask. Adult female: *a*, Forewing; *b*, hind tibia; *c*, vasiform orifice.

LECTOTYPE: Pupal case on slide mount in Maskell collection (labelled *melicyti*).

FOOD PLANT: *Melicytus ramiflorus* (W.M.M.).

TYPE LOCALITY: Auckland.

MATERIAL: One pupal case on cardboard (Maskell material of *melicyti*) in U. S. Bureau of Entomology. Five pupal cases on one slide mount (labelled *melicyti* by Maskell, 1878) in the Canterbury Museum.

Adult females and pupal cases were collected from *Melicytus ramiflorus* at Ruby Bay, Nelson, in January 1952. The pupal cases were sparse and few on a leaf and were dead and mostly parasitised.

Asterochiton cerata (Maskell)

Figs. 9, 10

Aleurodes cerata Maskell 1896: 425–6, pl. 26, fig. 1.

Aleyrodes cerata Mask. Cockerell, 1902: 281; Kirkaldy, 1907: 49; Quaintance, 1908: 5; Quaintance and Baker, 1914: 100.

LARVA: Described by Maskell (1896: 425). Specimen missing.

PUPAL CASE: (Fig. 9). Length 1.1 mm., width 0.7 mm. Shape elliptical flat. Dorsum covered with white flocculent wax, and a narrow ring of clear wax remains on leaf when case is removed. Colour yellowish-brown. Margin irregularly toothed. Thoracic tracheal folds not evident, thoracic tracheal pore (Fig. 10*a*) invaginated with comb of 2 or 3 teeth at bottom. Abdominal tracheal folds not evident, pore (Fig. 10*b*) and comb similar to thoracic. Setae: 8th abdominal, caudal and posterior marginal setae present. Submargin 0.03 mm. wide, delimited by line immediately mesad of which is a row of about 12 minute setae on each half and mesad of these a row of 60–65 minute circular pores. Sutures and segmentation faint. Pairs of faint paramedian pores on abdominal segments 1–7. Vasiform

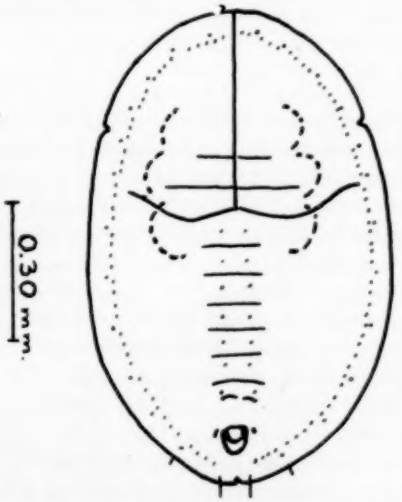


FIG. 9. *Asterochiton cerata* Mask. Pupal case, dorsal

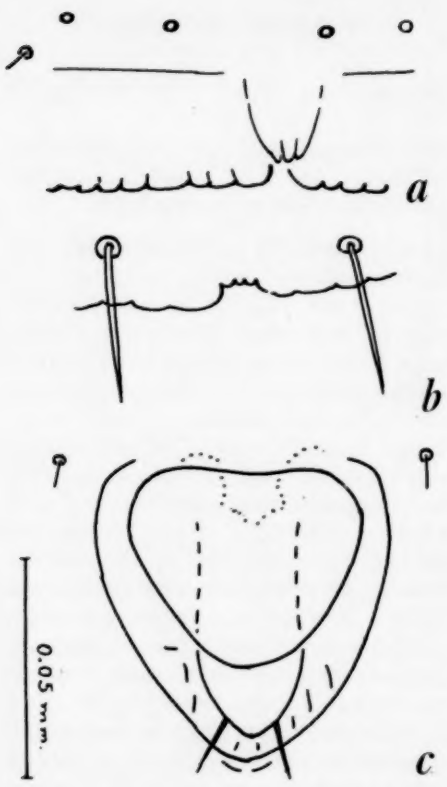


FIG. 10. *Asterochiton cerata* Mask. Pupal case: *a*, Thoracic tracheal pore; *b*, abdominal tracheal pore; *c*, vasiform orifice.

orifice (Fig. 10*c*) subcordate, 0.07 mm. long, 0.065 mm. wide, floor reticulate. Operculum subtriangular, 0.04 mm. long, 0.05 mm. wide more than half filling orifice. Lingula little constricted basally, bluntly pointed, with two strong apical setae.

ADULT: Unknown.

LECTOTYPE: Slide mount of pupal case (labelled larva) in Maskell collection.

FOOD PLANT: *Nothofagus menziesii*.

TYPE LOCALITY: Reefton. Collect. R. Raithby.

MATERIAL: One pupal case on Maskell slide mount (cotype) in U. S. Bureau of Entomology.

Duplicate unmounted material in Maskell collection. This species, which is not a typical *Aleurodes* but has the facies of *Asterochiton*, has been transferred by me to that genus.

Asterochiton fagi (Maskell)

Figs. 11, 12

Aleurodes fagi Maskell, 1890: 175, pl. 13, figs. 25, 26; 1896: 432.

Aleyrodes fagi Mask. Cockerell, 1902: 281; Kirkaldy, 1907: 53; Quaintance, 1908: 6.

Dialeurodoides fagi (Mask.) Quaintance and Baker, 1914: 99.

Asterochiton fagi (Mask.) Quaintance and Baker, 1915: xi.

LARVA: Unknown.

PUPAL CASE: (Fig. 11). Length 1.2 mm. Width 0.90 mm. Colour light yellowish-brown. Shape elliptical. Raised on vertical palisade of wax. Margin (Fig. 12*a*) irregularly

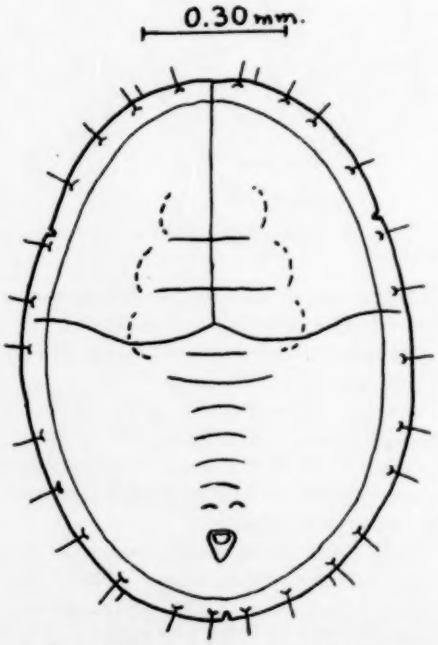


FIG. 11. *Asterochiton fagi* Mask. Pupal case, dorsal.

crenulate. Tracheal folds not evident. Thoracic tracheal pore (Fig. 12*b*) invaginated with two or three small teeth at bottom. Abdominal tracheal pore (Fig. 12*c*) similar. Anterior and posterior marginal setae present. Thirteen submarginal setae 0.10 mm. long on each side, based just mesad of margin, six on cephalothorax and 7 on abdomen. Minute setae on 8th abdominal segment. Caudal setae not differentiated from marginal setae. Disc without setae or prominent pores. Submargin separated from disc by line 0.07 mm. from margin. Vasiform orifice (Fig. 12*d*) 0.08 mm. long, 0.06 mm. wide, subtriangular, rather acute posteriorly. Operculum 0.05 mm. wide, 0.04 mm. long, sub-semicircular. Lingula slightly constricted basally, bluntly pointed apically, with two apical setae.

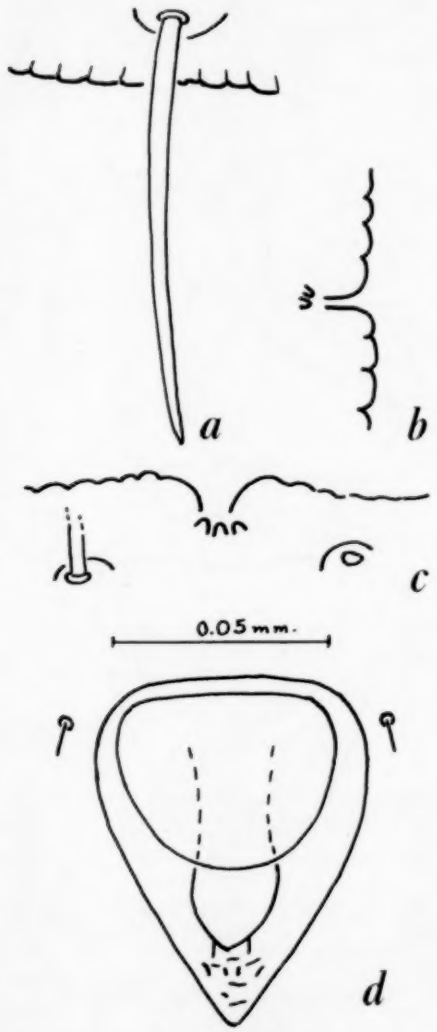


FIG. 12. *Asterochiton fagi* Mask. Pupal case: *a*, Margin; *b*, thoracic tracheal pore; *c*, abdominal tracheal pore; *d*, vasiform orifice.

ADULT: Unknown.

LECTOTYPE: Slide mount of pupal case in Maskell collection.

FOOD PLANT: *Nothofagus menziesii*.

TYPE LOCALITY: Inangahua. collect. R. Raithby.

MATERIAL: One pupal case on leaf (Maskell material) in U. S. Bureau of Entomology. Two pupal cases on leaf in Maskell collection. Unmounted Maskell duplicate material in Maskell collection. All or nearly all the material has been parasitised.

Asterochiton pittospori n. sp.
Figs. 13–15

LARVA: Unknown.

PUPAL CASE: (Fig. 13). Length 1.3 mm., width 1.0 mm. Colour white. Shape elliptical, flat. With a narrow fringe of white wax. Margin (Fig. 14*a*) is obscurely and rather irregularly toothed or crenulate. Thoracic tracheal fold (Fig. 14*b*) present, pore invaginated with a few or a group of teeth at bottom. Caudal fold absent, pore and comb (Fig. 14*c*) similar to thoracic. Anterior and posterior marginal setae present. Eight cephalothoracic discal setae as in *simplex*, one pair on first abdominal segment, one pair on fourth abdominal segment, one pair of minute setae on 8th abdominal segment and one pair of caudal setae of same size as other discal setae. Vasiform orifice (Fig. 14*d*) subtriangular, 0.7 mm. long, 0.6 mm. wide, floor reticulate. Operculum semicircular 0.05 mm. wide, 0.035 mm. long, half filling orifice. Lingula 0.04 mm.

long, finger-like, rounded apically, slightly constricted basally.

ADULT: *Female*, antenna (Fig. 15*a*) segment 3, 0.17 mm. long; 4, 0.04 mm.; 5, 0.05 mm.; 6, 0.04 mm.; 7, 0.05 mm., flagellum of 7 very short about ¼ as long as base. Wings (Fig. 15*b*) white, immaculate, forewing length 1.4 mm., R_1 absent. Hind tibiae with 22 setae in comb. *Male*, vasiform orifice (Fig. 15*c*) subcircular. Operculum 0.035 mm. wide, 0.015 mm. long, emarginate apically. Lingula finger-like, 0.035 mm. long, 0.009 mm. wide. Clasper (Fig. 15*c*) 0.12 mm. long, acutely pointed, rounded mesally at mid-length. Penis (Fig. 15*d*) in lateral view roundly angled at mid-length, subparallel sided, apically abruptly truncate and with slightly hooked tooth.

HOLOTYPE: Pupal case on slide mount deposited in Maskell collection.

TYPE LOCALITY: Pelorus Bridge. Collect. L. J. D. 20/10/51.

FOOD PLANT: *Pittosporum eugenioides*.

Closely related to *Asterochiton simplex* Maskell from the same food plant.

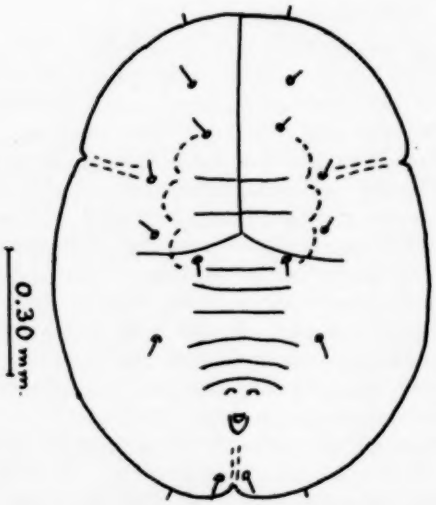
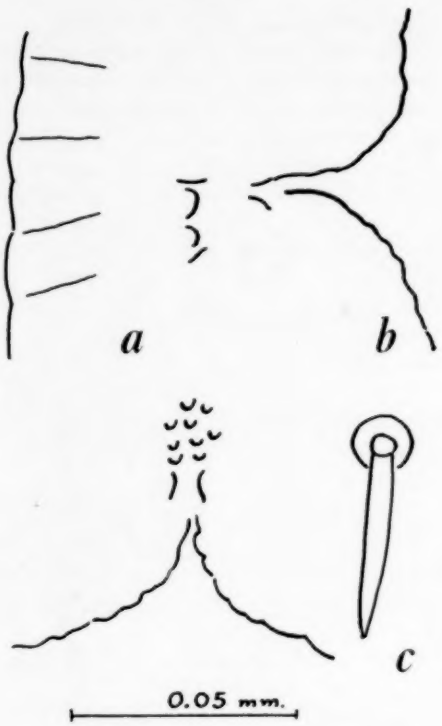


FIG. 13. *Asterochiton pittospori* n. sp. Pupal case, dorsal.



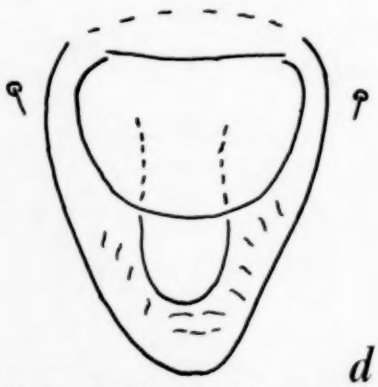


FIG. 14. *Asterochiton pittospori* n. sp. Pupal case: *a*, Margin; *b*, thoracic tracheal pore; *c*, abdominal tracheal pore; *d*, vasiform orifice.

Asterochiton simplex (Maskell)
Figs. 16–18

Asterochiton lecanioides Mask. (in part) 1879: 215–6.

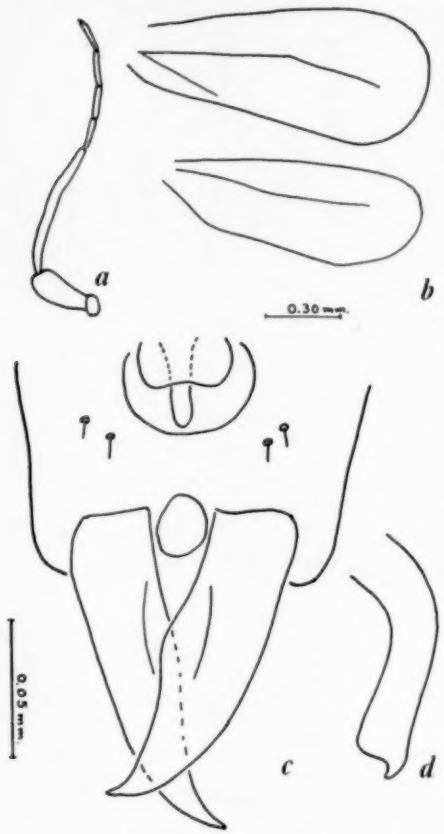


FIG. 15. *Asterochiton pittospori* n. sp. Adult female: *a*, Antenna; *b*, wings. Adult male: *c*, Vasiform orifice and claspers; *d*, penis, lateral view.

Aleurodes simplex Mask., 1890: 175–6, pl. 13, fig. 27; 1896: 441–2.
Aleyrodes simplex Mask. Cockerell, 1902: 281; Kirkaldy, 1907: 69; Quaintance, 1908: 7.
Dialeurodoides simplex (Mask.) Quaintance and Baker, 1914: 99.
Asterochiton simplex (Mask.) Quaintance and Baker, 1915: xi.

LARVA: Unknown.

PUPAL CASE: (Fig. 16). Length 1.2 mm., width 0.90 mm. Colour white. Shape elliptical, flat. With a narrow fringe of white wax. Margin (Fig. 17*a*) regularly crenulate, about 12 crenulations per 0.10 mm. Thoracic tracheal folds present but faint. Tracheal pore (Fig. 17*b*) invaginated with three or four irregular teeth at bottom. Abdominal tracheal fold, pore and comb (Fig. 17*c*) similar to thoracic. Submarginal area not differentiated. Posterior marginal setae present. Four pairs of setae on cephalothorax. One pair of setae on each of first, fourth, fifth, sixth and seventh abdominal segments. A pair of minute setae on 8th. Caudal setae same size as other abdominal setae. Vasiform orifice (Fig. 17*d*) subtriangular, 0.021 mm. long, 0.019 mm. wide, floor reticulate. Operculum subtriangular 0.015 mm. wide, 0.009 mm. long, not filling half orifice. Lingula finger-like, rounded apically, slightly constricted basally. Caudal furrow absent.

ADULT: *Female*, antennae (Fig. 18*a*) segment 1, 0.02 mm. long; 2, 0.06 mm.; 3, 0.165 mm.; 4, 0.03 mm.; remainder missing. Wings,

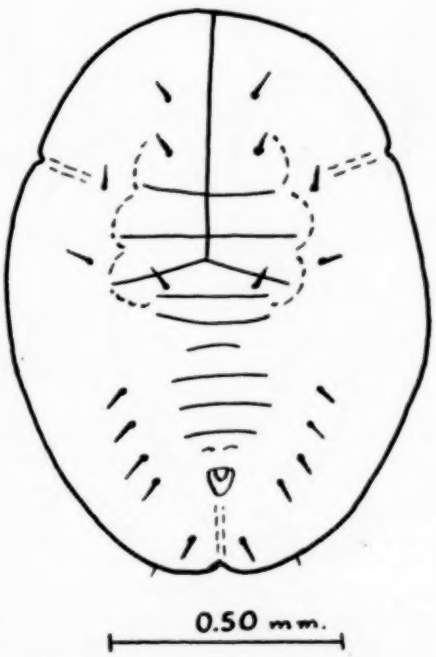


FIG. 16. *Asterochiton simplex* Mask. Pupal case, dorsal.

white, immaculate, forewing (Fig. 18*b*) 1.3 mm. long, R_1 absent. *Male*, vasiform orifice (Fig. 18*c*) subcircular. Operculum transverse, 0.04 mm. wide, 0.02 mm. long, emarginate apically. Lingula 0.03 mm. long, 0.01 mm. wide, finger-like, rounded apically, slightly constricted basally. Clasper (Fig. 18*d*) 0.155 mm. long, acutely pointed and with a slightly rounded hump at mid-length mesally. Penis (Fig. 18*e*) as in figure. Not abruptly truncate but tapering more gradually to base of tooth.

LECTOTYPE: Pupal case on slide mount in Maskell collection.

TYPE LOCALITY: Christchurch.

FOOD PLANTS: *Pittosporum eugenioides, Coprosma lucida* and several other trees.

MATERIAL: Two pupal cases (Maskell material) on leaf in U. S. Bureau of Entomology. Pupal material labelled *lecanioides* in Canterbury Museum. Unmounted duplicate material in Maskell collection.

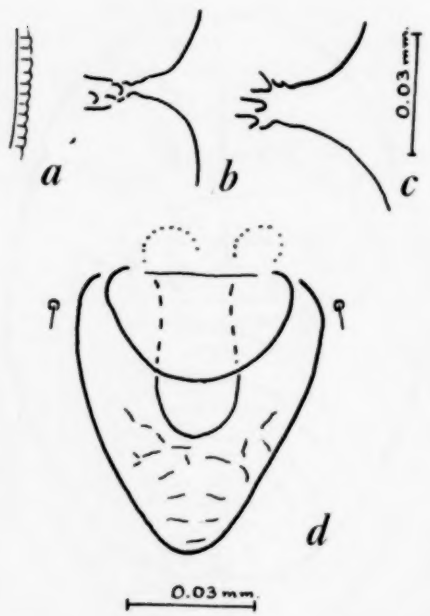


FIG. 17. *Asterochiton simplex* Mask. Pupal case: *a*, Margin; *b*, thoracic tracheal pore; *c*, abdominal tracheal pore; *d*, vasiform orifice.

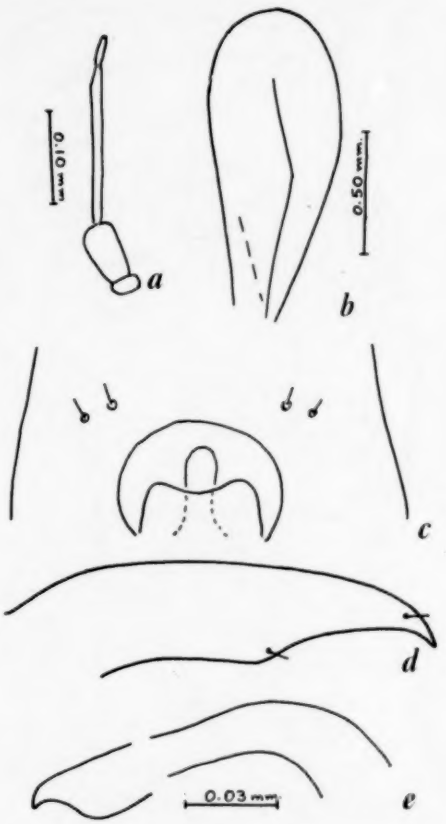


FIG. 18. *Asterochiton simplex* Mask. Adult female: *a*, Antenna; *b*, forewing. Adult male: *c*, Vasiform orifice; *d*, clasper; *e*, penis, lateral view.

Genus ALEYRODES Latreille

KEY TO PUPAL CASES OF NEW ZEALAND SPECIES OF *Aleyrodes*

Subcircular; 14 minute submarginal setae on each side; medial pigmentation light brown ..... **fodiens** Maskell

Broadly elliptical; 11 submarginal setae on each side; no pigmentation ..... **winterae** Takahashi

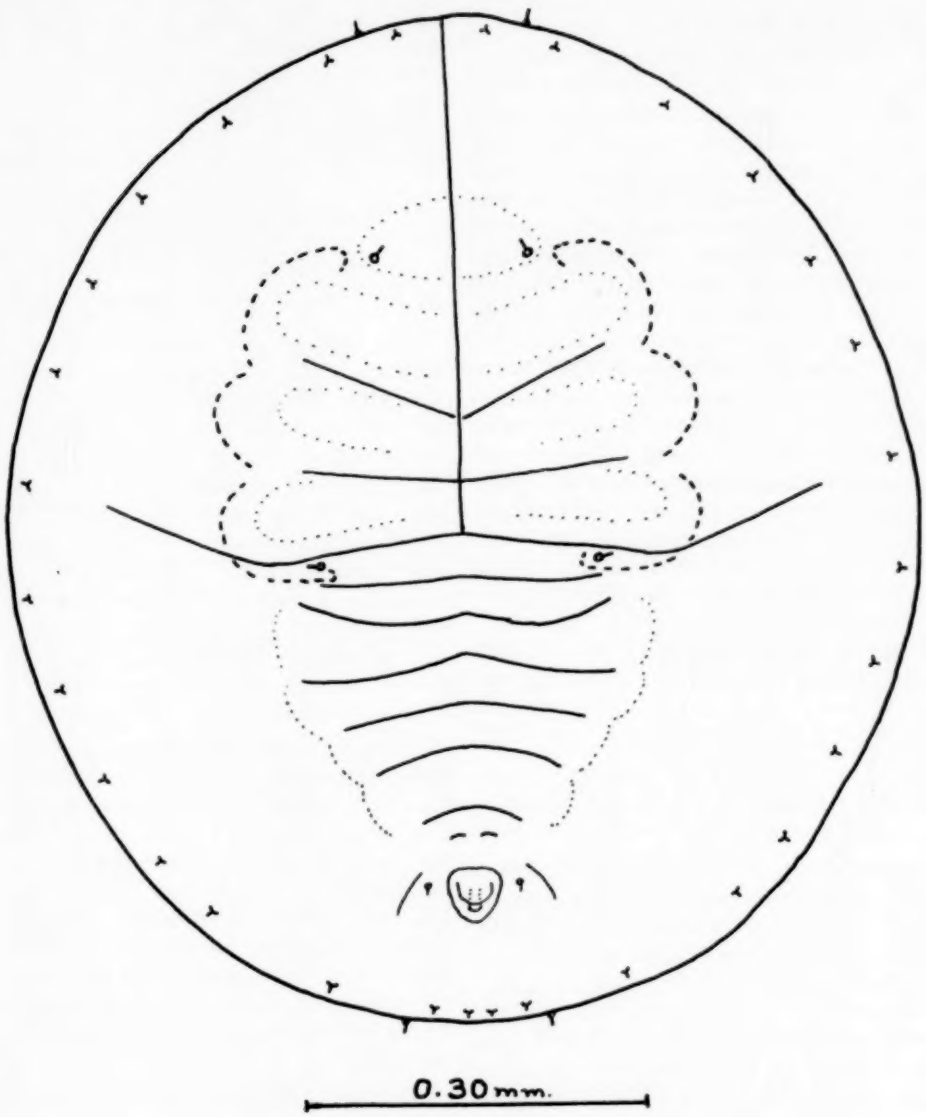


FIG. 19. *Aleyrodes fodiens* Mask. Pupal case, dorsal.

Aleyrodes fodiens (Maskell)
Figs. 19–21

Aleurodes fodiens Mask. 1896: 433–4, pl. 30, fig. 2; (Mask.) Cockerell, 1902: 281.

Aleyrodes fodiens (Mask.) Kirkaldy, 1907: 54; (Mask.) Quaintance 1908: 6.

Dialeurodes fodiens (Mask.) Quaintance and Baker, 1914: 97; Quaintance and Baker, 1917: 407, 415–416, pl. 66, figs. 1–4.

LARVA: Described by Maskell (1896) in

general terms. Slide missing.

PUPAL CASE: (Fig. 19). Length 0.87 mm., width 0.80 mm. Colour light brown in central disc and halfway to margins. Shape subcircular, flat. Margin obscurely and irregularly dentate, about 20 teeth in 0.10 mm. Thoracic and abdominal tracheal folds, pores and combs absent. Anterior and posterior marginal setae present. Fourteen minute submarginal setae on each half just mesad of margin. Submargin not delimited. One pair of minute setae on cephalic area, and on first and eighth abdominal segments. Caudal setae twice as long as marginal setae. Sutures and segmentation as in figure. Vasiform orifice (Fig. 20*a*) 0.062 mm. long, 0.05 mm. wide, subcordate, floor strongly reticulate, almost appearing to be toothed on posterior margin. Operculum 0.03 mm. long, 0.04 mm. wide, sub-semicircular, half filling orifice. Lingula little constricted, subparallel sided, rounded apically.

ADULT: *Female*, antenna (Fig. 20*b*); segment 3, 0.18 mm.; 4, 0.045 mm.; 5, 0.05 mm.; 6, 0.04 mm.; 7, 0.035 mm. Wings (Fig. 20*c*) white, unspotted, forewing 1.3 mm. long, stub of R_1 present. *Male*, operculum (Fig. 21*a*) length 0.02 mm., width apically 0.02 mm. wider basally, emarginate apically. Lingula rounded apically. Clasper (Fig. 21*a*) 0.15 mm. long, apex acute, prominent almost angulate bulge bearing two setae at mid-length mesally, four or five setae apically. Penis (Fig. 21*b*) subparallel sided in lateral view, abruptly angled to base of tooth which is fairly long and acute.

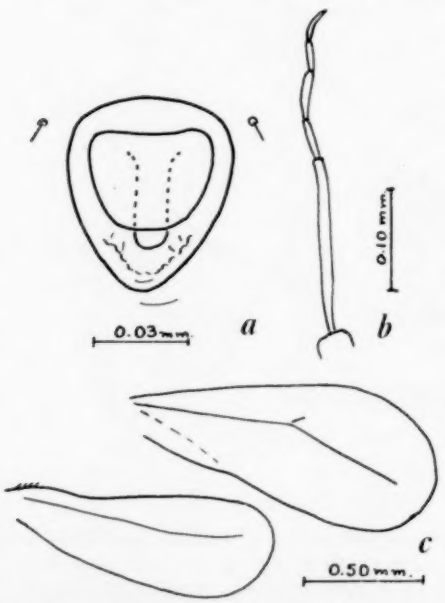


FIG. 20. *Aleyrodes fodiens* Mask. Pupal case: *a*, Vasiform orifice. Adult female: *b*, Antenna; *c*, wings.

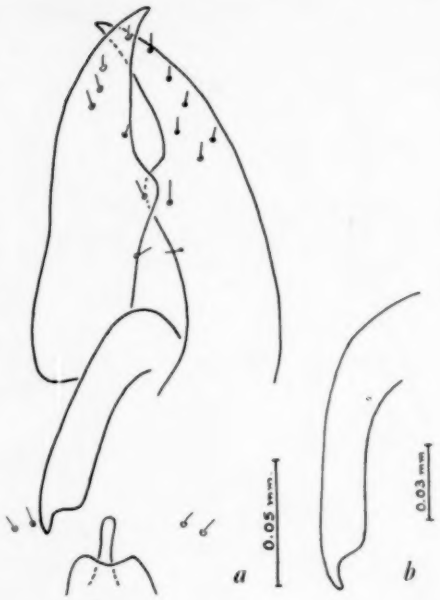


FIG. 21. *Aleyrodes fodiens* Mask. Adult male: *a*, Vasiform orifice, claspers, and penis; *b*, penis, lateral view.

LECTOTYPE: Pupal case on slide mount in Maskell collection.

TYPE LOCALITY: Reefton. Collect. R. Raithby.

FOOD PLANT: *Drimys* (*Wintera*) *axillaris*.

MATERIAL: Unmounted duplicate material in Maskell collection. Pupal cases and adults from *Wintera* at Waiho. Collect. L.J.D. 20/11/50.

Quaintance and Baker (1917) remark that *fodiens* is not a typical *Dialeurodes*. Although it is subcircular rather than oval and the lingula is not noticeably knobbed it would appear to fit the genus *Aleyrodes* best and I have returned it to that genus.

Aleyrodes winterae Takahashi

Figs. 22, 23

Aleyrodes winterae Takahashi 1937: 251–253.

LARVA: Unknown.

PUPAL CASE: (Fig. 22). Length 0.85–0.97 mm., width 0.72–0.81 mm. Colour light yellowish-brown. Shape subcircular, flat but slightly raised, sides not vertical. Margin (Fig. 23*a*) obscurely and irregularly crenulate. No thoracic or abdominal tracheal folds, pores or combs. Submargin indicated by a faint line anteriorly. Posterior marginal setae present. One pair of minute paramedian setae in cephalic region and one pair on each of the first and eighth abdominal segments. Ten submarginal setae on each side, six on the cephalothorax and four on the abdomen. Caudal setae not differentiated from submarginal setae. There are paired paramedian wrinkled areas on the anterior borders of abdominal segments 2–6 inclusive and also on the meso- and meta-thorax. Faint paired paramedian pores on abdominal segments 1–7. Vasiform orifice (Fig. 23*b*) 0.07 mm. long, 0.05 mm. wide, subtriangular, floor reticulate. Operculum 0.03 mm. long, 0.035 mm. wide, half filling orifice. Lingula finger-like, bluntly pointed, little constricted basally.

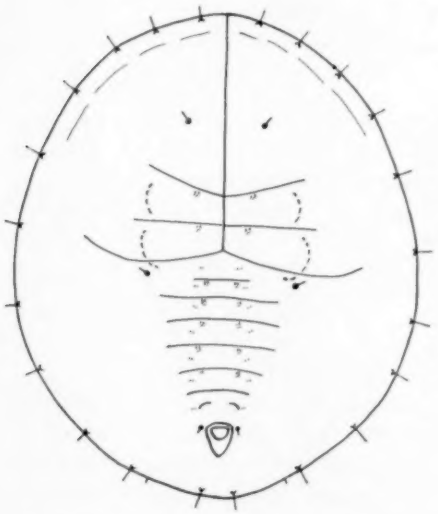


FIG. 22. *Aleyrodes winterae* Takahashi. Pupal case, dorsal.

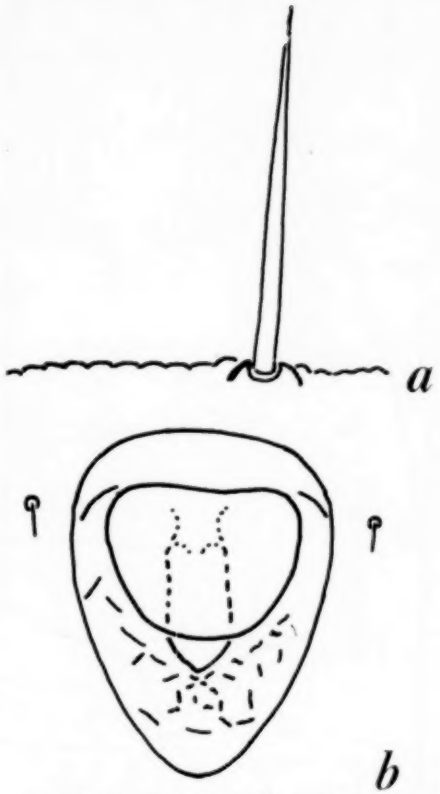


FIG. 23. *Aleyrodes winterae* Takahashi. Pupal case: *a*, Margin and seta; *b*, vasiform orifice.

ADULT: Unknown.

COTYPES: In the Department of Agriculture Research Institute, Formosa, and in the British Museum.

TYPE LOCALITY: Palmerston North. Collect. W. Cottier.

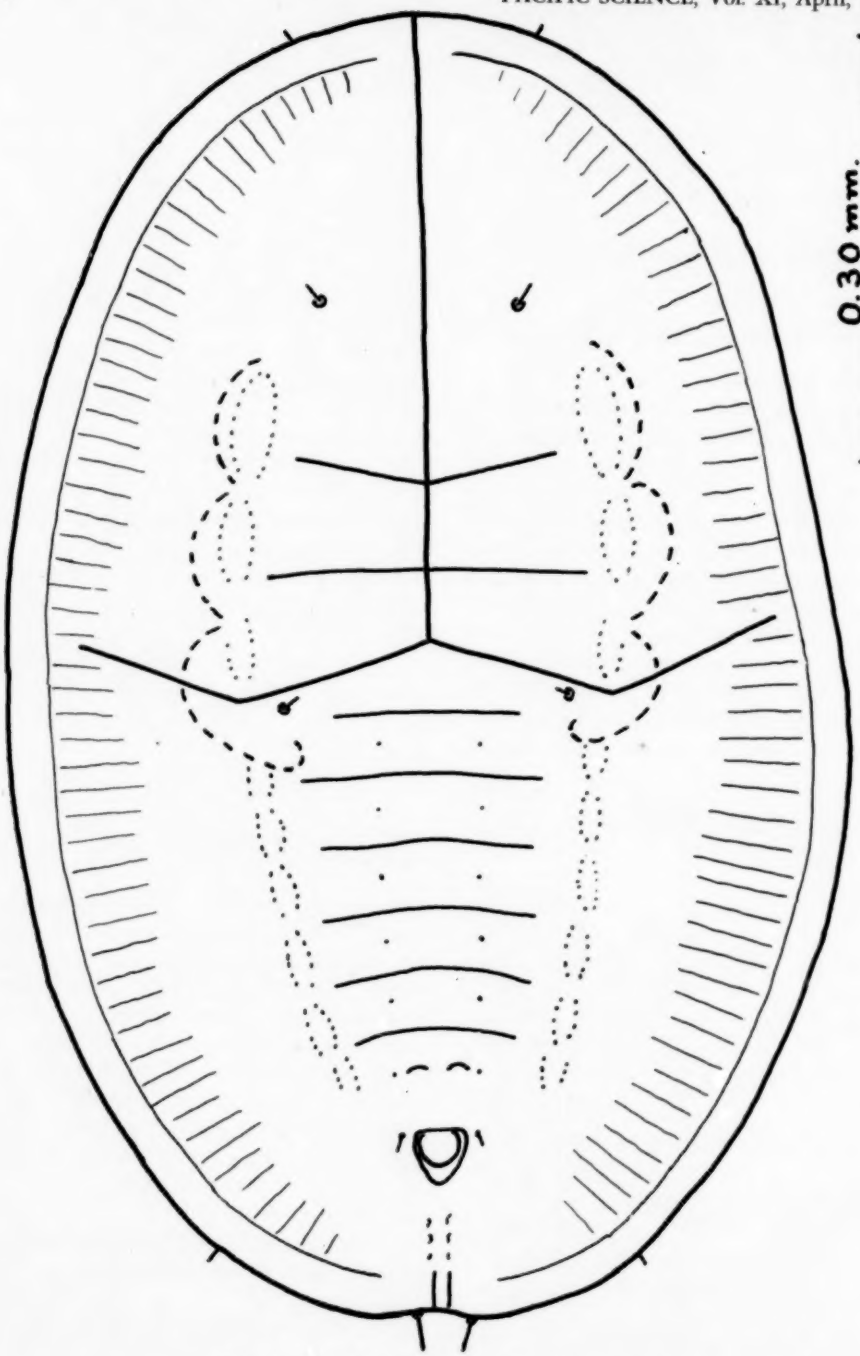


FIG. 24. *Aleuroclava eucalypti* n. sp. Pupal case, dorsal.

FOOD PLANT: *Wintera colorata*.

MATERIAL: Several specimens found in association with *fodiens* on *Wintera axillaris* in Maskell unmounted duplicate material collected by R. Raithby in Reefton.

This species is not a typical *Aleyrodes* according to Takahashi. It is evidently closely related to *fodiens*. The pupal cases are thicker and more raised than those of *fodiens*. Both species make shallow pits on the leaf.

Genus ALEUROCLAVA Singh

Aleuroclava eucalypti n. sp.

Figs. 24–26

LARVA: Unknown.

PUPAL CASE: (Fig. 24). Length 0.90 mm.–1.12 mm., width 0.56–0.71 mm. Colour white or colourless. Shape elliptical, flat. Margin (Fig. 25*a*) crenulated, 20–26 crenulations in 0.1 mm. Thoracic and abdominal tracheal folds, pores and combs absent. Submargin defined by submarginal line. Mesad of the submarginal line are faint radial depressed lines with between them radial rows of 7 or 8 tubercles of which the one nearest the margin is often larger. Segmentation as in figure. Thoracic area and abdominal segments 2–6 bounded laterally by a tubercular line. A pair of paramedian pores on each of abdominal segments 2–7. One pair of cephalic setae, one pair first abdominal, one pair 8th abdominal and one pair caudal 0.035 mm. long. Vasiform orifice (Fig. 25*b*) length 0.039 mm., width 0.036 mm. subcircular, raised above abdomen, toothed posteriorly and reticulate on floor. Operculum length 0.023 mm., width 0.028 mm., slightly subtrapezoidal, subtruncate apically. Lingula parallel sided, rounded apically, barely projecting beyond operculum, 0.02 mm. long. Anal furrow short, not extending halfway to orifice.

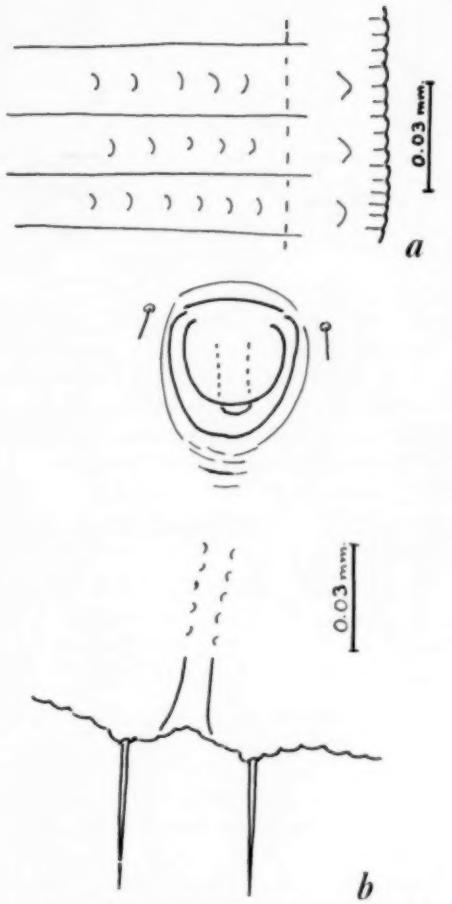


FIG. 25. *Aleuroclava eucalypti* n. sp. Pupal case: *a*, Margin; *b*, vasiform orifice and caudal margin and fold.

ADULT: *Female*, antennae: segment 2, 0.06 mm. long; 3, 0.14 mm.; 4, 0.04 mm.; 5, 0.045 mm.; 6, 0.035; 7, 0.045 base longer than flagellum. Wings white, immaculate, forewing 1.3 mm. long, R_1 present in some mounts, Rs present, Cu indistinct. Hind tibiae with comb of 16 setae. *Male*, operculum (Fig. 26*a*) 0.03 mm. wide, 0.015 mm. long. Lingula strap-shaped 0.025 mm. long, 0.005 mm. wide, projecting beyond orifice, subtruncate apically with corners angularly excised. Penis (Fig. 26*b*) length 0.11 mm., in lateral view, parallel sided, sinuate, truncate apically.

HOLOTYPE: Pupal case on slide mount deposited with Maskell collection.

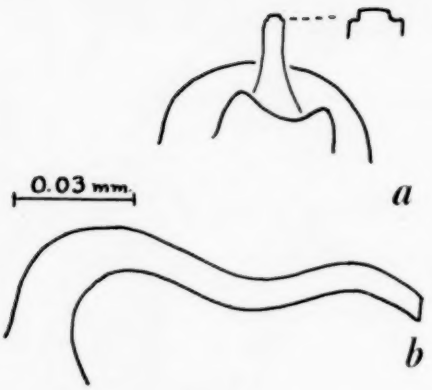


FIG. 26. *Aleuroclava eucalypti* n. sp. Adult male: *a*, Vasiform orifice; *b*, penis, lateral view.

TYPE LOCALITY: Waikakaho, Blenheim. Collect. L.J.D. 3/11/50.

FOOD PLANT: *Eucalyptus globulus*.

This species was almost certainly introduced into New Zealand with the food plant and therefore is of Australian origin.

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A Taxonomic Study of the Genus *Eugenia* (Myrtaceae) in Hawaii[1]

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THE PANTROPIC GENUS *Eugenia* (Myrtaceae) is represented in the forests of Hawaii by several species. A recent taxonomic treatment of the genus by Merrill and Perry (1939) divided the greater number of species of *Eugenia* into the genera *Syzygium* and *Eugenia* sensu strictu. A later study by Henderson (1947), based on the Malayan species, rejected this classification.

According to the Merrill and Perry classification, both *Syzygium* and *Eugenia* sensu strictu are present in the Hawaiian flora. Therefore, it seemed that an evaluation of the recent generic treatments based on these representatives would be of value. My study of the generic status of *Eugenia* and *Syzygium* led to the question of the specific status of the indigenous Hawaiian members. As a result of my investigations I have rejected the transfer of species of *Eugenia* to *Syzygium*, described a new species from the island of Molokai, and reduced two species and one variety to synonomy.

ACKNOWLEDGMENTS

Prof. Harold St. John suggested to me that the problem of the generic status of *Eugenia* was in need of further study. I have undertaken this problem under his guidance and am indebted to him for his help and encouragement. I wish to thank Miss Marie C. Neal, Curator of the Herbarium of the Bernice P. Bishop Museum, for her helpful and valuable assistance and for the opportunity to work on the specimens in the herbarium. Dr. Rogers McVaugh, Curator of Phanerogams of the Herbarium of the University of Michigan, has generously made the space and facilities of the herbarium available to me for continuing this study. I gratefully acknowledge the assistance of Dr. Joseph F. Rock, who provided valuable information based on his knowledge and experience with the Hawaiian flora.

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HISTORY OF THE GENUS

Since Linnaeus' treatment of *Eugenia* in *Species Plantarum* (1753: 470), more than 800 species have been described or transferred to this genus. Many botanists have been dissatisfied with the wide range of difference in form shown by the members of the genus.

[1] Part of a thesis submitted to the Graduate School of the University of Hawaii in partial fulfillment of the requirements for the degree of Master of Science.

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One of the most comprehensive reclassifications of *Eugenia* was proposed by Niedenzu (1893). He established several segregate genera which were based mainly on the characters of the flower. His system was adopted by many workers, but, because of the lack of distinct generic limits, many other botanists continued to consider *Eugenia* in a broader sense. Later studies of the members of the group led more and more botanists to reject Niedenzu's classification and to return the segregated genera to *Eugenia*.

Because of the great number of species described in *Eugenia* the group has become rather unwieldy, and Merrill and Perry (1938*a*, 1938*b*, 1939) proposed a new systematic treatment of the group. They redefined some of the earlier proposed segregates of the genus. The new systematic treatment which they proposed is based on the structure of the seed. According to them, species of *Eugenia* are diagnosed as having a pericarp which is easily crushed and "the seed is free, the testa is smooth, chartaceous to cartilaginous and mostly lustrous, and the cotyledons are mechanically inseparable, i.e., they have grown together in such a way that often the line of their opposing faces is scarcely distinguishable." *Syzygium*, one of the segregate genera, is described as having "fruits that when dried are not too easily broken, and, when opened, the embryo (not the entire seed) falls out leaving the roughish seed coat more or less loosely adhering to the pericarp; the embryo has two distinct cotyledons usually attached near the middle of the opposing faces which conceal the hypocotyl within."

In a monograph of the species of *Eugenia* in Malaya, R. M. Henderson (1949) critically analyzed Merrill and Perry's classification. Henderson, in his study, decided that neither the degree of adherence of the seed coat to the cotyledon, nor the nature of the cotyledons themselves is consistent enough to be regarded as a good generic character. In fact, he gives detailed descriptions of the seeds of several different species which illustrate an intergrading series from those with two distinct and separate cotyledons to those with the cotyledons completely fused. On the basis of these observations he rejects the transfer of species from *Eugenia* to *Syzygium*.

In 1953 Ingle and Dadswell published the results of their studies of the wood anatomy of several Pacific Myrtaceae.[3] They concluded that the anatomy of the wood of *Eugenia* provides ample characters for splitting the genus. They added that the "suggested split on anatomical grounds involved only the two groups *Eugenia A* [corresponding to *Eugenia* sensu strictu] and *Eugenia B* [including the genera *Acmena*, *Cleistocalyx* and *Syzygium*]."[4]

The most recent treatments of the genus have been inconsistent. By far the majority of workers (Airy Shaw, 1949; Backer, 1945; Degener and Ludwig, 1952) have accepted Merrill and Perry's classification without any apparent critical study. A few botanists (White, 1945; Amshoff, 1942), seemingly in doubt as to the validity of this system, have hesitated to adopt it.

EVALUATION OF THE RECENT GENERIC TREATMENTS

The Hawaiian flora, although predominantly Asiatic in its affinities, includes representatives of the tropical regions of both the Old World and the New World. Because of the uniqueness of the Island flora in this respect, the Hawaiian Islands may be considered an ideal region for evaluating the recent treatment of *Eugenia*.

The two most important features used by Merrill and Perry in segregating the genera are: (1) the nature of the embryo, and (2) the degree of adherence of the testa to the cotyledons. On the basis of these characters

[3] See also Dadswell and Ingle, 1947.

[4] Since this paper went to press Kathleen M. Pike published the results of her studies in the pollen morphology of the Myrtaceae. (*Austral. Jour. Bot.* 4(1): 13–53, 1 pl., 1956.) She found that the pollen grains of "*Eugenia* A" are distinct from those of "*Eugenia* B" and thereby adds support to the groupings of Ingle and Dadswell based on the wood anatomy.

Merrill and Perry (1938*a*, 1938*b*, 1939), in studies of Indo-Chinese, Chinese, and Bornean species of *Eugenia*, redefined the group, placing most of the species of those regions in the genus *Syzygium*. Geographically, their new concept limits *Eugenia* mainly to tropical America, and *Syzygium* primarily to the tropics of the Old World.

The genus *Eugenia* in the Hawaiian Islands is represented by eight species as I interpret them. In my opinion, according to the Merrill and Perry system, four of the Hawaiian representatives of *Eugenia* would be classified in the segregate genus *Syzygium*, while four would fall in *Eugenia* sensu strictu.

Eugenia malaccensis and *E. Jambos* have fruits which contain a rather large seed loosely attached within the pericarp. In both species the embryo has two distinct, fleshy cotyledons. The surface of the cotyledons is very rugose and the thick seed coat adheres firmly to it. Young seedlings of *E. malaccensis* were found growing which had the two cotyledons still attached. The pericarp had rotted away and no evidence of it could be seen, but on the surfaces of the cotyledons remains of the seed coat were still present.

In fruits of *Eugenia Cumini* the fleshy pericarp peels off, leaving the seed coat firmly adhering to the cotyledons. The cotyledons are fleshy and distinct. In dried, raw fruits the seed coat readily peels off with the pericarp. However, when boiled, the pericarp may be easily removed without disturbing the seed coat.

Upon removal of the pericarp the testa of *Eugenia sandwicensis* also remains attached to the cotyledons. The two fleshy cotyledons are not consolidated. In boiled dried material, depending on the amount of care given it, the pericarp may or may not peel away from the seed coat.

The seeds of *Eugenia rariflora* and *E. koolauensis* have their cotyledons plainly separated, partly fused, or entirely consolidated. When the cotyledons are consolidated the line of their opposing faces is not evident. In both dried and fresh fruits the thin seed coat peels off with the pericarp.

On the basis of the studies I have made, it seems evident that neither the character of the seed coat nor that of the embryo offers a satisfactory basis for the reclassification of the group. Neither one of the characters is constant. The degree of fusion of the cotyledons varies even within a single species.

The conclusions I have drawn on the basis of investigations of the Hawaiian representatives of *Eugenia* strongly support Henderson's rejection of the segregation of species of *Eugenia* into the genera *Syzygium* and *Eugenia* sensu strictu.

No attempt was made to study the wood anatomy of the Hawaiian species of *Eugenia*. In view of Ingle and Dadswell's findings (1953) I suggest that additional more extensive investigations may reveal other morphological characters to support their conclusions. The characters of the seed, since they are so variable, do not justify the split.

VARIATION AND DISTRIBUTION OF THE SPECIES IN HAWAII

The genus is represented in Hawaii by only four indigenous species, three of which are endemic. Of these four, *Eugenia rariflora* and *E. sandwicensis* show the greatest degree of variation within the entire group. Both show variations in leaf size ranging from very small to rather large.

The greatest degree of variation is seen in *Eugenia sandwicensis*. The forms of *E. sandwicensis* with the larger leaves are found most often on Kauai; the forms with elliptical and elliptical-lanceolate leaves are more prevalent on Maui, and most of the Oahu representatives have the smaller obovate leaves. On Lanai the majority of the representatives of this species have small obovate leaves similar to those of the most common forms on Oahu. Most of the members on Molokai have leaves which resemble the forms on Maui, although in general they are not as long. It is possible

for a person who is familiar with the species to determine, in the majority of cases, from which one of the islands a specimen was collected. However, this broad generalization of geographical distribution is not constant, and almost all forms are present on each of the islands where the species occurs.

Of the naturalized species *Eugenia Cumini* is by far the most widely distributed. *E. malaccensis* is confined mostly to shaded, moist valleys where it is likely they were planted originally by the Hawaiians. Both *Eugenia Jambos* and *E. uniflora* are only sparsely distributed in the native forests.

These introduced species are remarkably constant in their characters and show no significant degree of variation.

EXPLANATIONS

Unless otherwise indicated, the specimens studied are in the Bernice P. Bishop Museum. The standard abbreviations of Lanjouw and Stafleu (1954) are used to indicate the locations of the other specimens:

BISH—Bernice P. Bishop Museum, Honolulu
GH—Gray Herbarium, Cambridge
K—Royal Botanical Gardens, Kew
M—Botanische Staatssammlung, München
MICH—University of Michigan, Ann Arbor
NY—New York Botanical Gardens, New York
US—United States National Herbarium, Washington

I have examined the following numbers of fruits and seeds of the species included in this problem. When possible both fresh and dried material was studied.

	Fresh	*Dried*
Eugenia malaccensis	15	3
E. Jambos	—	5
E. sandwicensis	100	60
E. Cumini	50	20
E. uniflora	10	5
E. rariflora	—	15
E. koolauensis	20	10

TAXONOMY

Eugenia L., Sp. Pl. 470, 1753.

Syzygium Gaertn., Fruct. 1: 166, t. 33, 1788. *Jambosa* DC., Prodr. 3: 286, 1828.

Trees or shrubs. Shoots glabrous or pubescent. Leaves simple, opposite, glandular-punctate, pinnately veined with a continuous intramarginal vein. Leaf scar with a single vascular bundle. Flowers single or in pairs, axillary, or in terminal, or axillary cymes or racemes, or inflorescence on leafless branches. Calyx tube[5] globose to elongate-turbinate, extending beyond the ovary or not so, usually minutely glandular-punctate; calyx lobes 4, large persistent and spreading, or small and early deciduous; petals 4, free and spreading persistent or caducous, or cohering and falling off as a calyptra; stamens numerous, free on a staminal disk lining the calyx tube or inserted on the margin of the calyx tube; anthers versatile, cells splitting longitudinally, connective gland present; style filiform, stigma small; ovary inferior, 2-celled. Fruit a berry with only 1 seed (rarely 2) developing from the many ovules, crowned by the persistent calyx lobes or by the truncate scars of the calyx lobes; umbilicus sometimes present; seeds large with a thin membranaceous or a thick cartilaginous or fibrous seed coat; cotyledons thick, fleshy, completely free or partly or entirely fused.

Type species: *Eugenia uniflora* L.

KEY TO THE SPECIES IN HAWAII

A. Flowers in cymes or racemes; calyx tube extending beyond the ovary.
  B. Calyx tube 10–30 mm. long.
    C. Inflorescence axillary from older leafless nodes or rarely from leafy

[5] "Calyx tube" is used here, as is customary in treatments of the genus, to refer to the inferior ovary and especially to the tissues adhering to it. There is no intention to imply the exact morphological nature of the inferior ovary of *Eugenia* by the use of this term. The origin of the inferior ovary in this genus has not as yet been satisfactorily determined.

nodes; petals not reflexing at anthesis; stamens 1–2 cm. long; leaves 5–9 cm. wide, elliptical to obovate-oblong . . . . . **1. E. malaccensis**

C. Inflorescence terminal; petals reflexing at anthesis; stamens 2–5 cm. long; leaves 2.5–5 cm. wide, linear-lanceolate . . . . **2. E. Jambos**

B. Calyx tube 3–8 mm. long.

D. Stamens 20–30, included in the calyx tube, inflexed, 0.5–1.5 mm. long; fruit pink to deep red . . . . . **3. E. sandwicensis**

D. Stamens more than 50, exserted, spreading, 3–7 mm. long; fruit dark purple or black . **4. E. Cumini**

A. Flowers single or in pairs, axillary; calyx tube not extending beyond the ovary.

E. Fruits longitudinally 8-ribbed; calyx lobes membranaceous . . **5. E. uniflora**

E. Fruits not ribbed; calyx lobes fleshy.

F. Leaves flat or slightly concave, glabrous beneath or only sparingly puberulent near midrib . . . . . **6. E. rariflora**

F. Leaves strongly concave and with the entire lower surface puberulent.

G. Fruit orange-yellow; flowers with punctiform pistil . . . . . **7. E. koolauensis**

G. Fruit red; flowers with peltate pistil . . . . . **8. E. molokaiana**

1. **Eugenia malaccensis** L., Sp. Pl. 470, 1753.

Jambosa malaccensis (L.) DC., Prodr. 3: 286, 1828.

Syzygium malaccense (L.) Merr. and Perr., Arnold Arboretum, Jour. 19: 215, 1938.

Tree 8–20 m. tall; branches greyish-brown, smooth, glabrous; leaf scars 3–6 mm. wide, lunate-elliptic, pale; bundle scar large, transverse; leafy branches brown, glabrous, 3–5 mm. in diameter, angled or terete; internodes 1.5–6 cm. long; leaves 14–25 cm. long, 5–9 cm. wide, elliptical to obovate-oblong, apex abruptly acute or obtuse, base cuneate to abruptly cuneate; margin entire or slightly undulate; blade coriaceous, above glabrous, shiny, dark green, sparsely black punctate, below pale, glabrous, minutely black punctate; midrib light green, shallowly impressed above, elevated below; primary lateral veins alternate or opposite, 8–14 on a side 1–2.5 cm. apart, irregularly ascending at 140–150°, meeting in a conspicuously sinuate, continuous intramarginal vein 0.5–1.5 cm. from leaf margin, smaller, continuous intramarginal vein 1–2 mm. from leaf margin, irregularly lobed, raised or impressed above, elevated below; the veinlets less distinct, raised-reticulate; petioles 1–1.5 cm. long, 3–4 mm. wide, reddish-green, glabrous; cymes axillary or on stems below leaves 2–5 cm. long; peduncle 5–10 mm. long, angled or terete, glabrous, reddish-green, pedicels when present, 2–8 mm. long, glabrous, reddish-green, articulate, but some flowers sessile; calyx tube green to reddish-green, 1–3 cm. long, 1–1.5 cm. wide, obconic, elevated above ovary, narrowing into a short pseudostalk 0.5–1.0 cm. long, subtended by 2 deltoid bracts 1–1.5 mm. long; calyx lobes 4, persistent, broad, rounded, 2–3 cm. long, 6–8 cm. wide, green; petals 4, spreading, obovate-orbicular, pink to red, glabrous, deciduous, glandular-punctate, 6–9 mm. long, 7–10 mm. wide, apex rounded or acuminate, base truncate; stamens numerous (about 100), exserted, 1.0–2.0 cm. long; filament slender, red, glabrous, terete above, flattened below; anthers white 9–12 mm. long, oblong; style red, subulate, 1.5–2 cm. long, glabrous; ovary 2-celled multiovulate; fruit obovoid 5–7.5 cm. long, 4–6 cm. in diameter, pinkish to dark red, umbilicate on top, crowned with truncate scars of the calyx lobes or calyx lobes persisting;

pericarp crisp, watery, 1.0–2.0 cm. thick; seed loosely attached within, subglobose, 1.5–2.0 cm. in diameter; seed coat fibrous, brown, 1 mm. thick, adhering closely to the rugose surface of the cotyledons; cotyledons 2, white or greenish, equal or unequal, not fused.

Common name: "Ohia ai," Mountain Apple.

DISTRIBUTION: Common in the moist gulches on the larger islands. Native to the Indo-Malayan region, it may now be found in cultivation, widely distributed in the tropics of the world.

Specimens examined:

HAWAIIAN ISLANDS: *Hillebrand and Lydgate; Mann and Brigham 119; U. S. Explor. Exped.* (NY).

KAUAI: Waioli Valley, along stream, alt. 100 m., Feb. 27, 1927, *MacDaniels 909.*

OAHU: Punaluu, stream bank, elev. 800 ft., Sept. 28, 1930, *St. John 10,581* (NY); Punaluu Valley, in dark forest in wet ground at bottom of Pig God trail, Sept. 2, 1932, *Degener 7,349;* Waikane-Schofield trail, side of trail, 1000 ft. alt., Dec. 2, 1951, *Wilson 46;* Koolauloa, Kaluanui, Sacred Falls Valley 700 ft. alt., May 18, 1952, *Wilson and Doty 137, 138, 139, and 141;* Kipapa Gulch, frequent at bottom of gulch, in "koa zone," *Egler 37–421;* Kalihi Valley, Jan. 1, 1920, *Garber 97;* Moanalua Valley, March 7, 1910, *Forbes 1465.0;* Kaumokunui Gulch, rich dark wet gulch at 1500 ft., April 13, 1936, *Degener 11,887* (NY, MICH); Waianae Mts.: Makaleha Valley, Jan. 14, 1929, *Neal;* Puu Kaupakuhale, 2nd gulch of N.E. slope of Puu Kaala, in wood, May 14, 1933, *St. John 13,173.*

MOLOKAI: Mapulehu, April 1910, *Rock.*

MAUI: Kailua, Haleakala, April 1911, *Rock.*

HAWAII: Hilo, May 1909, *Faurie.*

Eugenia malaccensis was most likely introduced into the Hawaiian Islands by the Polynesians. It may be found growing in large groves in moist, shaded valleys where it was probably originally planted and has subsequently become established.

2. **Eugenia Jambos** L., Sp. Pl. 470, 1753.

Jambosa Jambos (L.) Millsp., Field Mus. Nat. Hist., Bot. Ser. 2(1): 80, 1900.

Syzygium Jambos (L.) Alston, in Trimen, Fl. Ceyl. 6 (Suppl.): 115, 1931.

Tree 6–10 m. tall; branches brown to yellowish-brown, glabrate, longitudinally ridged; leaf scars rounded shield-shaped, 2.5–4 mm. wide, pale; stems of leafy branches 3–4 mm. in diameter, 4-angled or compressed, becoming terete in age, glabrous; internodes 1.5–3 cm. long; leaves 10–20 cm. long, 2.5–5 cm. wide, lanceolate or oblong-lanceolate, tapering to an acuminate apex, base cuneate; margin entire; blade coriaceous, above olive-green to reddish-green, glabrous, shiny, minutely pustulate, below paler, glabrous, minutely glandular-punctate; midrib shallowly impressed above, elevated below, light yellowish-green to reddish-green; primary lateral veins alternate or opposite, 10–15 on a side, 5–15 mm. apart, slightly elevated above, very prominent below, straight or slightly curved ascending at 140–150°, meeting in an irregularly lobed continuous intramarginal vein 3–5 mm. from leaf margin; the veinlets obscure above, distinctly raised-reticulate below; petiole 5–10 mm. long, 2–3 mm. wide, glabrous, dark reddish-green; racemes terminal, 6–10 mm. long, rachis 6–15 mm. long, 3–4 mm. wide, 4-angled brownish-green to reddish-green, glabrous; pedicels 7–15 mm. long, flower single on the pedicels, 3–6 cm. long, 6–8 cm. in diameter; calyx tube obconic, 1–1.5 cm. long, 7–10 mm. wide, elevated above ovary, narrowed into a short pseudostalk, glabrous or sparsely puberulous, minutely glandular-punctate, green or yellow-green, subtended by 2 caducous, glabrate, subulate bracts 0.8–1.0 mm. long; calyx lobes 4, persistent, fleshy, unequal, 1 pair 6–8 mm. long and 8–9 mm. wide, the smaller pair 4–6 mm. long, 8–9 mm. wide, below minutely glandular-punctate, glabrous or sparsely puberulous; petals 4, white to greenish-white, orbicular to ovate-orbicular, concave, spread-

ing, glandular-punctate, 1–1.7 mm. in diameter, glabrous; stamens numerous (about 200), creamy-white, 1–5 cm. long; filament slender, terete, creamy-white, glabrous; anthers white, oblong, 1–2 mm. long; style terete, subulate, 3–4 cm. long, glabrous, creamy-white to greenish-white, exserted or included; fruit subglobose, 2–4 cm. tall, 4–6 cm. wide, yellow or pinkish-yellow, minutely glandular-punctate, umbilicate on top, crowned by persistent calyx lobes, style often persistent; pericarp fleshy, 1–1.5 cm. thick; seed loosely attached within, subglobose, 2–2.5 cm. in diameter; seed coat 1 mm. thick, brown, coriaceous, closely adhering to the surface of the cotyledons; cotyledons white or greenish-white, equal or unequal, not fused.

Common name: "Ohia loke," Rose Apple.

DISTRIBUTION: Sparingly naturalized on probably all of the larger islands of Hawaii. Widely distributed in the tropics of the world.

Specimens examined:

KAUAI: Kokee Camp, becoming naturalized, July 5, 1926, *Degener 7,341* (NY); Waioli Valley, along stream, alt. 50 m., Feb. 27, 1927, *MacDaniels 908.*

OAHU: Waikane-Schofield trail, Waikane, 750 ft. alt., side of road, Dec. 2, 1951, *Wilson 45;* Waiahole, Jan. 23, 1909, *Rock 1,285 and 1,287;* Manoa, near Woodlawn, spreading locally, Apr. 1937, *Egler 37–423.*

MAUI: Iao Valley, Wailuku, roadside, elev. 800 ft., Feb. 9, 1930, *St. John 10,277* (BISH, NY).

HAWAII: Naturalized, *Degener 7,344;* South Kona, Honomalina, Ranch House, near Kona highway, 1800 ft. alt., Sept. 7, 1952, *Chock 768;* near Glenwood, naturalized in pasture, June 23, 1929, *Degener 7,343* (NY).

Degener (1932–34) records that *Eugenia Jambos* was probably first introduced into Hilo from Rio de Janeiro by Mr. Bridge in 1853. It may now be found growing along road and trail sides and in other moist areas. Although Degener also records it as "definitely known from Kauai, Molokai, Oahu, Maui and Hawaii," no specimens of it were seen from Molokai.

3. **Eugenia sandwicensis** Gray, U. S. Explor. Exped. Bot. (official ed.) 519, 1854.

Syzygium sandwicense (Gray) Ndz., in Engl. and Prantl Pflzfam. 3(7): 85, 1893.

Eugenia sandwicensis var. *parvifolia* Hdb., Fl. Hawaii. Is. 129, 1888.

Syzygium oahuense Deg. and Ludw., Bot. Staatsaml. München, Mitt. 4: 113, 1952.

Tree or shrub, 3–25 m. tall; branches greyish-brown to reddish-brown, glabrous; leaf scars 1–4 mm. wide, rounded, shield-shaped, reddish-brown to yellowish-brown; young leafy branches green to reddish-green, glabrous, 1–4 mm. in diameter, distinctly 4-angled, angles winged; wings 0.2–2.0 mm. wide, branchlets becoming terete with age, dark red to reddish-brown bark scaling off in longitudinal strips exposing yellow-grey to reddish-yellow bark beneath; internodes 1–5 cm. long; leaves 2–14 cm. long, 1.5–5.0 cm. wide, obovate, ovate, elliptic or ovate-lanceolate, apex acute, obtuse, retuse, or apiculate, base truncate to cuneate, blade coriaceous, flattened or concave, margin entire, slightly revolute (rarely strongly so), above dark green or yellowish-green, shiny, glabrous, minutely glandular-punctate, below paler, dull, glabrous, minutely glandular-punctate, midrib pink to dark red, shallowly impressed above, elevated below; primary lateral veins alternate or opposite, 15–30 on a side, 2–8 mm. apart, irregularly ascending at 100–115°, meeting in an irregularly lobed intramarginal vein 0.5–1.5 mm. from leaf margin, raised on both surfaces but more distinct below; the veinlets raised-reticulate; petioles 2–10 mm. long, 1–2 mm. wide, reddish-brown, glabrous, cymes simple or compound, in axils of upper leaves, 5–8 cm. long; peduncle 2.5–3.5 cm. long, 1.5–3 mm. wide, 4-angled, winged, yellow-green to reddish-green, pedicels 2–4 mm. long, articulate; calyx tube turbinate, 3–4

mm. long, 3.5–5 mm. wide, glabrous, reddish-green to yellow-green, minutely glandular-punctate, subtended by two deciduous, glabrous, deltoid bracts 1–2 mm. long; the 4 calyx lobes 0.5 mm. long, imbricate, obtuse, reddish-green to dark red, early deciduous; petals 4, white to greenish-white, spreading, soon deciduous, usually discrete but sometimes united and falling off as a calyptra, ovate or obovate, often emarginate, glabrous, glandular-punctate, apex subacute or obtuse, base truncate, 2–3 mm. long, 2–3 mm. wide; stamens (about 30) inserted on the margin of the calyx tube, 0.5–1.5 mm. long, introrse, included; filaments white to pinkish, subulate, glabrous; anthers white 0.4–0.8 mm. long, orbicular-ovate; pistil white to reddish, glabrous, slender, 0.8–1.5 mm. long, included; ovules 4–10 in a cell; fruit light pink to dark red, 4–10 mm. high, 5–10 mm. wide, glabrous, shiny, minutely glandular-punctate, globose or elliptic, flattened on top, crowned by truncate scars of the calyx lobes; pericarp fleshy, 1–1.5 mm. thick; seed globose, elliptic or oblong-elliptic; seed coat reddish-brown, 0.5 mm. thick, loosely adhering to the pericarp, closely adhering to the smooth surface of the cotyledons; cotyledons equal, greenish or white, conspicuously glandular-punctate, not fused.

Type: U. S. Explor. Exped. "Oahu, Sandwich Islands; on the mountains behind Honolulu" (US).

Common name: "Ohia ha," known on Maui as "Paihi."

DISTRIBUTION: Endemic to the Hawaiian Islands. Found in the moist forests on Kauai, Oahu, Molokai, Lanai, and Maui; not known from the island of Hawaii.

Specimens examined:

KAUAI: Waimea, Alakai Swamp trail, 3800 ft. alt., rain forest, Dec. 25, 1952, *Wilson 206;* on Kaholuamanu above Waimea, Sept. 2–9, 1895, *Heller 2,241;* Kaholuamanu to Waimea, Oct. 27, 1916, *Hitchcock 15,558* (US); near Kaholuamanu, Kauluwehi Swamp, Oct. 25, 1916, *Hitchcock 15,520* (US); Wahiawa Mts., *Lydgate;* Wahiawa Mts., August 1909, *Forbes 181.K;* Wahiawa, Kahili Swamp, 2100 ft. alt., Lihue-Koloa Forest Reserve, Dec. 29, 1930, *St. John et al. 10,850;* Koloa, Laaukahi ridge, ¼ mile north of N.W. facing slope, 850 ft. alt., moist wooded gulch, Dec. 24, 1947, *St. John, Webster and Wilbur 23,007;* Laaukahi, Haiku, 1300 ft. alt., dense woods on precipitous slope, Dec. 22, 1933, *St. John and Fosberg 13,486;* Ka Loko Reservoir (Kilauea), Oct. 8, 1916, *Forbes 544.K;* E. fork of Kilauea River, rain forest, alt. 400 m., Feb. 11, 1927, *MacDaniels 654;* Wainiha, Wainiha Valley, moist lower forest, 800 ft. alt., Jan. 1, 1934, *St. John and Fosberg 13,929;* Wainiha, Wainiha Valley, 1000 ft. alt., on bank, side of road, in native forest, Dec. 31, 1952, *Wilson 235;* Hanakapiai, Napali Coast, forest on cliff, Jan. 2, 1931, *St. John et al. 10,992;* Hanakoa, Waiahuakua Stream, 350 ft. alt., Dec. 31, 1952, *Wilson and St. John 238;* Hii Mts., Oct. 22, 1916, *Forbes 652.K.*

OAHU: No locality: *Mann and Brigham 204; Hillebrand* (received July 1865) *311* (GH) (locality illegible, probably Oahu); *U. S. Explor. Exped.* (US). Koolau Mts.: Kahuku Army trail, July 1930, *Russ;* Hauula, Kaipapau Forest Reserve, Maakua-Papali ridge, wooded ridge, 1200 ft. alt., *St. John 13,372;* Kahana Valley, head of, Hauula Forest Reserve, 1000 ft. alt., lower woods, Dec. 10, 1933, *St. John 13,410;* Kahana Valley (south side of), ridge *mauka* of church, dense forest at 1500 ft., Nov. 5, 1950, *Degener and Silva 21,069* (US); Kahana Valley, head of, 1500 ft. alt., Aug. 31, 1924, *Harris;* Kaipapau on S. slope of ridge, 2500 ft. alt., Oct. 15, 1933, *Suehiro;* Punaluu, Dec. 3–4, 1908, *Rock 632 and 687* (GH), and *526;* Punaluu, Dec. 24–29, 1908, *Rock 377* (GH); Punaluu, Dec. 3, 1908, *Rock 149* (GH); Punaluu, wet mountain side, Nov. 30, 1929, *Tanaka;* Punaluu to Kaipapau, May 8–13, 1909, *Forbes;* Punaluu to Kaipapau, May 3–8, 1909, *Forbes and Cooke*, and *Forbes and Thompson;* Punaluu to Kaipapau, Nov. 14–21, 1908, *Forbes;* Kahana, Kaluanui, open woods, 2000 ft. alt., Nov. 30, 1929, *St. John*

10,099 (US); Waikane-Schofield trail, Waikane, 750–1250 ft. alt., Oct. 16, 1932, *Krauss;* Waikane-Schofield trail, near summit, 2000–3000 ft. alt., Sept. 16, 1932, *Yuncker 3,186* (US); Waikane-Schofield trail, 2200 ft. alt., Dec. 2, 1951, *Wilson 44;* north ridge of Kaaawa Valley, April 12, 1931, *St. John 11,085;* Heeia, Haiku Valley, Waiahole Forest Reserve, 500 ft. alt., in *Dicranopteris* thicket on ridge, Dec. 11, 1932, *St. John 12,260;* Konahuanui, Jan. 16, 1909, *Forbes 1,040;* Konahuanui—*Forbes 1,003*, and *1,309*, *Bryan 208*, *MacDaniels 124*, and *Heller 2,241* (US, MICH); Pupukea Military trail, Jan. 29, 1927, *MacDaniels 549;* Waimea-Malaekahana, 1900 ft. alt., March 22, 1953, *Ozaki 391*, *392*, *390*, *and 389;* Paalaa, South Opaeula Gulch, Nov. 9, 1930, *St. John 10,630;* Waipio, Kipapa Gulch, wet high mountain ridge, Nov. 10, 1929, *Tanaka;* Waipio, Kipapa Gulch, E. of Puu Kamana, wooded ridge, 1700 ft. alt., May 15, 1932, *St. John 11,683;* Waipio, Kipapa Gulch, south ridge, wooded slope, 1300 ft. alt., Nov. 10, 1929, *St. John 10,037;* Waipio, Kipapa Gulch, south ridge, 1400 ft. alt., woods, Oct. 29, 1929, *St. John 9,965;* Kawailoa, Kawaiiki Ditch trail, alt. 1340–1000 ft., Nov. 2, 1947, *Wilbur 257* (US); Kawailoa, Kawaiiki Ditch trail, moist *Metrosideros* forest, 1050 ft. alt., Jan. 17, 1953, *St. John 24,973;* Kawailoa, Kawaiiki Ditch trail, Aug. 15, 1922, *Skottsberg 230;* Kawailoa trail, rain forest, Oct. 31, 1937, *Hartt;* Kalauao ridge, Ewa Forest Reserve, moist woods, March 29, 1933, *St. John 13,028;* Halawa ridge trail, in moist forest, April 25, 1948, *Cowan 973; mauka* of Red Hill, in forest, Oct. 9, 1932, *Degener 7,328* (US, MICH); Kalihi-Nuuanu ridge, alt. 550 m., Jan. 23, 1927, *MacDaniels 156;* Kalihi-Nuuanu, Puu Lanihuli, main ridge running S.W. from Kalihi-Nuuanu, wooded ridge, 1600 ft. alt., Nov. 29, 1931, *St. John 11,176;* Kalihi-Nuuanu, Lanihuli trail, Sept. 17, 1908, *Forbes;* Lanihuli trail, Nov. 14, 1908, *Forbes;* Lanihuli trail, Dec. 10, 1908, *Forbes;* Nuuanu-Kalihi ridge, Aug. 13, 1922, *Skottsberg 156;* slope *mauka* from Tantalus, alt. 600 m., Nov. 1, 1926, *MacDaniels 98;* Pauoa, Konahuanui trail, Feb. 15, 1921, *Garber 229;* Pauoa flats, 1926, *Skottsberg 1,783;* Manoa, slopes back of Woodlawn, on crest of ridge, alt. 1000 ft., Dec. 31, 1942, *Kuykendall 49;* Olympus trail, alt. 700 m., Dec. 21, 1926, *MacDaniels 125;* Palolo-Manoa ridge, alt. 350 m., Dec. 21, 1926, *MacDaniels 122*; Palolo Valley, near first falls of Palolo, Nov. 16, 1919, *Garber 70;* Palolo Valley, Oct. 22, 1914, *Forbes 1929.0;* ridge between Palolo and Waialae-iki, Jan. 30, 1917, *Forbes 2411.0;* Palolo-Waialae ridge, Jan. 27, 1927, *MacDaniels 484 and 487;* Wiliwilinui ridge, 1600 ft. alt., March 16, 1952, *Wilson 106*, *108*, *111*, *113*, *115*, *116*, *117*, *118*, *119*, *and 120;* Niu Valley, summit ridge, Aug. 22, 1909, *Rock 4,840*. Waianae Mts.: Dupont trail, northern slope of Kaala, Feb. 29, 1949, *Degener et al. 19,428;* Dupont trail, north slope of Mt. Kaala, 2800 ft. alt., rain forest, Sept. 10, 1950, *Hatheway et al. 344;* eastern part of Kaala summit, Sept. 25, 1938, *Degener et al. 12,247* (NY); Kaala, Oct. 13, 1929, *Yoshinaga;* Mokuleia, 1200 ft. alt., July 18, 1924, *Wilder 1,287;* Makaha Valley, Feb. 12–19, 1909, *Forbes;* Honouliuli, ridge above Kupehau, dry brushy slope, alt. 650 m., June 30, 1935, *Fosberg 10,986;* Palehua, Aug. 23, 1922, *Skottsberg 207;* slope south of Palawai Gulch, *ca.* 2700 ft., March 27, 1948, *Wilbur 602*.

MOLOKAI: Olokui, 3000 ft. alt., ridge between upper forks of Wailele stream, rain forest, Feb. 6, 1948, *St. John and Wilbur 23,343;* Halawa, ridge south of valley, Aug. 1912, *Forbes 477.Mo.* (US); Kaluaaha, April 1910, *Rock 7,060* (GH); Kaluaaha, rain forest, June 28, 1928, *Degener 7,323* (GH); Pukoo, June 1910, *Faurie 434*.

LANAI: Aug. 1913, *Munro 15;* Sept. 1917, *Forbes 361.L* (US); Waiakeahua Gulch, in decadent, deer devastated forest at 2500 ft., Aug. 4, 1949, *Degener and Murashige 20,322* (US); Waiakiola Valley, July 28, 1910, *Rock 8,056* (GH): Kaiholena, *Munro 6;* Lanaihale, July 28, 1940, *Degener 12,976* (US); Puu Aalii, Kealia Aupu-Kaunolu divide, lower forest,

April 14, 1938, *St. John 18,851;* mountains near Koele, June 1913, *Forbes 78.L;* mountains near E. end, June 1913, *Forbes 275.L.*

MAUI: Makawao, Oct. 1910, *Rock 8,617* (US); April 1911, *Curran 62* (US); upper ditch trail Haleakala, Oct. 13, 1922, *Skottsberg 808;* Kailua, north slope of Haleakala, June 13, 1920, *Forbes 2499.M* (US); Kailua, Dec. 25, 1908, *Rock;* Kipahulu, 2500 ft. alt., Kaukaua Gulch, west ridge, summit of, *Acacia Koa* woods, Dec. 28, 1936, *St. John and Catto 17,806;* Nahiku, July 1910, *Forbes;* along ditch near Oopuola stream, lower rain forest, July 7, 1927, *Degener 7,324* (US); Puu Kukui, upper forest, 3–5000 ft., Sept. 25, 1916, *Hitchcock 14,804* (US); near where trail leaves tunneled stream for Mt. Eke climb, rain forest, Aug. 27, 1927, *Degener and Wiebke 2,307* (US, MICH).

This species exhibits extreme variation, especially in the leaves. The leaves are of various shapes, with a great number of intermediate forms, and they range in size from 14 × 5 cm. to 2 × 1.5 cm. The obovate leaf with an obtuse apex is most frequently encountered, but even on a single branch with leaves predominantly of this shape, others with ovate leaves and acute apices may be found. Of all the characters the flowers are the most constant.

No combination of characters was found on which a separation of the various forms could be based. Any attempt at reclassifying the group always disclosed intergrading forms which rendered the system impractical.

The absence of this widely distributed species on the island of Hawaii is peculiar. Rock (1913*a*) lists this species as occurring "on all islands of the group," but no single collection of it was found from Hawaii.

4. **Eugenia Cumini** (L.) Druce, Bot. Exch. Club Brit. Is., Rpt. 3: 418, 1914.

Myrtus Cumini L., Sp. Pl. 471, 1753.
Eugenia Jambolana Lam., Encycl. 3: 198, 1789.
Syzygium Cumini (L.) Skeels, U. S. Dept. Agr., Bul. 248: 25, 1912.

Tree 6 to 20 m. tall; branches pale yellowish-grey, glabrous, in age the bark greyish-white; leaf scars 2–4 mm. wide, rounded shield-shaped, yellowish-grey; leafy branchlets 1–3 mm. in diameter, terete or slightly angled, glabrous, pale brown to greyish-white; internodes 1.5–4.5 cm. long; leaves opposite, 7–18 cm. long, 3–8 cm. broad, oblong-ovate to elliptic-oblong, apex shortly or abruptly acuminate, rarely obtuse, base broadly cuneate narrowing toward petiole, margin entire or slightly undulate, blade coriaceous, above olive-green, minutely glandular-punctate, glabrous and shiny, below dark yellowish-green, dull, minutely pitted or pustulate, glabrous; midrib shallowly impressed above, elevated below; primary lateral veins numerous, alternate or opposite, 25–40 on a side, 2–5 mm. apart, irregularly ascending at 140–150°, meeting in an irregularly lobed intramarginal vein 1–3 mm. from leaf margin, raised on both surfaces; the veinlets raised-reticulate; petioles 1–2.5 mm. long, 1 mm. wide, glabrous; inflorescence cymose, on previous years' branches or occasionally in axils of the leaves, rarely terminal, 4–12 cm. long; peduncle 1–3 cm. long, terete or slightly angled, glabrous, subtended by two deciduous, subulate bracts 0.5–1.5 mm. long, glabrous; pedicels decussate, articulate, slender terete or slightly angled, subtended by one deciduous subulate bract; flower sessile, calyx tube campanulate, 3–5 mm. long, 2–3 mm. across, brownish-pink, glabrous, finely glandular-punctate, narrowing into a stout psuedostipe, subtended by 2 deciduous bracts; bracts reddish-brown, deltoid, 1–1.5 mm. long; calyx lobes 4, quickly deciduous; petals 4, white, minutely glandular-punctate, orbicular, concave, 2–3 mm. in diameter, falling off as a calyptra; stamens numerous (about 100), exserted and spreading, inserted on the margin of the calyx tube; filaments pinkish, 2–6 mm. long, slender, subulate, glabrous, finely glandular-punctate, anthers white, 3–7 mm. long, orbicular-ovate; style terete, subulate, included, 5–6.5 mm. long, glabrous, finely

glandular-punctate; berry oblong to oblong-elliptic, asymmetric 1.5–2.0 cm. long, 1.0–1.5 cm. wide, glabrous, dark purple or black, shiny, minutely glandular-punctate, umbilicate, crowned by the truncate scars of the calyx lobes, umbilicus 1–2 mm. tall, 1.5–3 mm. in diameter; pericarp pulpy, 1.5–3 mm. thick, seed ellipsoid or oblong-ellipsoid, 1.0–1.5 cm. long, 0.5–1.0 cm. wide, seed coat, crustaceous, 0.5–1.0 mm. thick, closely adhering to the subrugose surface of the cotyledons; cotyledons unequal, not fused, conspicuously glandular-punctate.

Common name: Java Plum.

DISTRIBUTION: Widely distributed on all the Hawaiian islands, found in large stands in dry and moist valleys; cultivated, spreading from cultivation, and established. Widely distributed in the Indo-Malayan region and in the tropics of the world.

Specimens examined:

KAUAI: Hanapepe, Koula Valley, 750 ft. alt., on side of road, Dec. 27, 1952, *Wilson 210.*

OAHU: Koolau Mts.: Honolulu, Nuuanu Valley, Dowsett Highlands, by road, Sept. 19, 1943, *Neal.* Waianae Range: Kamananui, Dupont trail on ridge south of Pamoa Gulch, by forest reserve fence, 1500 ft. alt., Sept. 14, 1952, *Wilson 145;* N. of Kaala, naturalized in pasture, April 26, 1937, *Degener 11,902 and 11,903* (NY); Mokuleia, Makaleha Valley, 900 ft. alt., in lowland scrub, Sept. 15, 1950, *Hatheway et al. 357;* Honouliuli, Puu Manawahua, lower woods, 1800 ft. alt., Sept. 29, 1929, *St. John 9,893.*

MOLOKAI: Halawa Valley, 150 ft. alt., spreading along trail, by abandoned, overgrown taro patches, Dec. 27, 1932, *St. John et al. 12,676;* eastern side of Wailau Valley near ocean, naturalized, Aug. 14, 1928, *Degener 9,664* (NY); near Kanalo, naturalized, Aug. 8, 1928, *Degener 7,345* (NY).

MAUI: Wailuku, culta, Aug. 1909, *Faurie 55;* Muolea, E. Maui, 3 miles from Hana, along roadside, Dec. 27, 1951, *Wilson 101;* Ukumehame, Ukumehame Gulch, 800 ft. alt., along bank of stream, Dec. 29, 1951, *Wilson 104.*

HAWAII: Puna, Pahau Nui, alt. about 1700 ft. associated with guava, Aug. 2, 1945, *Fagerlund and Mitchell 1,104;* above Hilo, along Malili stream, homestead, alt. 650 m., *MacDaniels 249.*

Eugenia Cumini is of recent introduction into the Hawaiian Islands. It has rapidly become established and widely distributed, most likely by birds which relish the fruit. It may now be found in abundant stands in the dryer regions of the islands, forming the dominant vegetation of valleys with periodically dry streams.

No record has been found that indicates when this species was introduced into the islands. The earliest collection of it in the Hawaiian Islands was by Faurie on Maui in August 1909. He records it as "Wailuku Culta."

5. **Eugenia uniflora** L., Sp. Pl. 470, 1753.

Shrub 2–3 m. tall, branches greyish-brown, smooth, glabrous; leaf scars 1–1.5 mm. wide, rounded shield-shaped, yellow-brown to reddish-brown; leafy branches green to greyish-brown, glabrous, 1–4 mm. in diameter, angled when young, becoming terete in age; internodes 2–4 cm. long; leaves 4–7 cm. long, 2–4 cm. wide, ovate to ovate-lanceolate, tapering to acuminate apex, base rounded to subcuneate; margin entire, slightly revolute; blade thin coriaceous, above glabrous, shiny yellow-green to dark olive-green, minutely glandular-punctate, below pale yellow-green, glabrous or very sparsely puberulous, minutely glandular-punctate; midrib reddish-green, shallowly impressed above, elevated below; primary lateral veins alternate or opposite, elevated on both surfaces but more conspicuous below, 9–12 on a side, 4–7 mm. apart, irregularly ascending at 140–150°, meeting in an irregularly lobed continuous marginal vein 2–5 mm. from leaf margin; less conspicuous continuous or sometimes interrupted marginal vein 0.5–1 mm. from leaf

margin; the veinlets less distinct, raised-reticulate; petioles 2–5 mm. long, 0.5–1 mm. wide, dark reddish-green, glabrous; flowers single or in pairs, axillary; peduncles 2–4 cm. long, 4-angled or terete, glabrous; calyx tube 2–3 mm. long, 3–4 mm. wide, green, glabrous or sparsely puberulent; calyx lobes 4, persistent, 3–4 mm. long, 3–4 mm. wide, membranaceous, green, ovate with acute apex, ciliate, minutely glandular-punctate, attached to annular disk within the tube; petals 4, white, spreading, persistent, obovate with an obtuse apex, ciliate, 7–8 mm. long, 5–6 mm. wide, sparsely glandular-punctate; annular disk raised 0.5 mm. above point of petal insertion, strigose; stamens numerous (about 50), spreading, inserted on annular disk; filaments 3–7 mm. long, white glabrous, subulate; anthers white, 0.5–1 mm. long, orbicular-ovate; style, terete, subulate, slightly exserted or included, 4–6 mm. long, glabrous; fruit subspherical, red, 1–2 cm. high, 1–2 cm. wide, glabrous, minutely glandular-punctate, crowned by the persistent calyx lobes, conspicuously longitudinally 8-ribbed; pericarp fleshy, 2–3 mm. thick; seed subglobose, 8–15 mm. in diameter, seed coat thin membranous, loosely adhering to the pericarp or to the surface of the cotyledons; cotyledons fused, finely glandular-punctate.

Common name: Surinam Cherry, Pitanga.

DISTRIBUTION: Very sparingly naturalized on the larger islands. Native to Brazil.

Specimens examined:

KAUAI: Lihue, planted, June 10, 1926, *Degener 2,080*.

OAHU: U. S. Expt. Station, Oct. 25, 1926, *MacDaniels 349*.

MOLOKAI: Halawa Valley, 50 ft. alt., shrubs by roadside, Dec. 27, 1932, *St. John et al. 12,665*.

HAWAII: Planted and persisting, April 10, 1930, *Degener 7,331* (NY).

The number of collections of this species is very meager, and future collections should be made to establish the occurrence of it in the Hawaiian Islands.

6. **Eugenia rariflora** Benth., in Hooker's London Jour. Bot. 2: 221, 1843.

Eugenia waianensis Deg., Fl. Hawaii., Fam. 273, 7/15/32.

Eugenia koolauensis Deg. var. *glabra* Deg., Fl. Hawaii., Fam. 273, 8/10/32.

Eugenia rariflora Benth. var. *parvifolia* Hdb., Fl. Hawaii. Is. 129, 1888.

Tree or shrub 3–7 m. tall; branches grey to greyish-white, glabrous, in age the bark greyish-white to greyish-brown, longitudinally and transversely irregularly furrowed; leafy branchlets 1.5–2 mm. in diameter, quadrangular to terete, brown, brown puberulent when young; leaf scars rounded shield-shaped, 1–1.5 mm. wide; bundle scar 1; internodes 0.5–3 cm. long; leaves opposite, 3–7 cm. long, 1.5–5 cm. wide, blade elliptical, ovate or obovate, apex obtuse, acute, retuse or apiculate, base cuneate or rounded, coriaceous, above olive-green, shiny, minutely glandular-punctate, glabrous or sparsely puberulent near midrib, below dull, yellowish-green, minutely pustulate, glabrous or somewhat puberulent at base near midrib; midrib shallowly impressed above, elevated below; primary lateral veins alternate or opposite, 5–3 on a side, 4–8 mm. apart, irregularly or straight ascending at 140–150°, meeting in an irregularly lobed intramarginal vein, 1–2 mm. from leaf margin, raised on both surfaces, but more distinct below; the veinlets raised-reticulate; petioles 2–4 mm. long, 1 mm. wide, brown, glabrous or slightly puberulent; flowers single or in pairs, axillary; peduncles 5–15 mm. long, glabrous or puberulent; calyx tube 2–3 mm. long, 3–4 mm. across, obconic, brown, puberulent, minutely glandular-punctate, subtended by two persistent, subulate sparsely puberulent bracts 1–1.5 mm. long; calyx lobes 4, unequal in length, 1 opposite pair 3–4 mm. long, 3–4 mm. wide, the other pair shorter, 2–3 mm. long, 3–4 mm. wide, ovate, green, fleshy, persistent, below minutely glandular-punctate, glabrous, above glabrous, within the tube attached to annular

disk; petals 4, white, spreading, persistent, 6–8 mm. long, 4–5 mm. wide, inserted on the margin of the disk, ovate, obovate or elliptic, minutely glandular-punctate, membranaceous, ciliate and sparsely puberulous, apex obtuse or acuminate, base truncate; annular disk raised 0.5 mm. above point of petal insertion, glabrous; stamens numerous (about 150), inserted on disk; filaments white, 1.5–5 mm. long, slender, subulate, glabrous; anthers white, 0.5–0.8 mm. long, orbicular-ovate; style terete, subulate, slightly exserted or included, 2–4 mm. long, glabrous; fruit ovoid to subspherical, crowned by persistent calyx lobes, 1–2 cm. high, 1–1.6 cm. wide, glabrous or somewhat appressed-pilosulous, red, orange or yellow, minutely glandular-punctate; pericarp fleshy, 1–2 mm. thick, seed globose, 8–10 mm. in diameter; seed coat thin membranous, closely adhering to the pericarp; cotyledons 2, white or yellowish, minutely glandular-punctate, usually fused, but sometimes only partly fused or entirely free.

Lectotype: "Feejee Islands" (Fiji) *Hinds 1841* (K).

Common name: "Nioi" (Rock, 1913*b*).

DISTRIBUTION: High islands of Polynesia. In the Hawaiian Islands it is found on all the large islands except the island of Hawaii.

Specimens examined:

KAUAI: Hanakoa, 750 ft., Aug. 28, 1926, *Judd 44;* Haupu, Kipu, 800 ft. alt., wooded slope, Dec. 25, 1933, *St. John and Fosberg 13,616;* northeast of Kipu, June 17, 1926, *Degener 7,304* (NY).

OAHU: Koolau Mts.: Waimano, 6–1919, *Russ;* Waimano, E. branch, E. slope above pass, May 29, 1933, *Russ;* Waimano, Oct. 1935, *Meebold* (*Degener 20,768*) (M); ridge between Niu and Wailupe, April 11, 1917, *Forbes 2458.0.* Waianae Mts.: Near Kawaihapai, shaded dry slope, Jan. 27, 1929, *Degener and Bush 7,305* (GH, NY); Mokuleia, Kaawa (= Kaawa?) Gulch, north of Kaala, dryish forest slope, Aug. 2, 1938, *Degener and Odonez 12,192* (US, NY); Mokuleia, west side of east branch of E. Makaleha stream, 1300 ft. alt., steep talus slope, in dryland forest, Aug. 31, 1950, *Hatheway 376;* Mokuleia, east side of east branch of Makaleha Valley, densely forested slope at 1600 ft., July 2, 1950, *Degener, Hatheway and Greenwell 20,824* (US); Mokuleia, west branch of E. Makaleha Valley, 1800 ft. alt., dry forest on steep valley side, June 11, 1952, *St. John 24,827;* Mokuleia, west branch, E. Makaleha Valley, in small side gulch, 1750 ft. alt., Sept. 30, 1950, *Hatheway 384;* Makaleha Valley, May 2, 1918, *Rock 17,005* (GH); Makaleha Valley, Oct. 23, 1936, *Meebold* (*Degener 21,980*) (M); Mokuleia, gulch southwest of Dillingham Ranch, in shade at 1700 ft., April 23, 1950, *Degener, Hatheway and Carrol 20,615;* Mokuleia, 4th gulch east of Puu Kaupakuhale, Kamananui, Puu Kaala, Oct. 23, 1932, *Yuncker and Hosaka 3,216* (US); half mile southwest of Pohakea Pass, single, dying tree on dry grass and lantana covered slope, July 30, 1932, *Degener and Bush 4,194* (GH); Honouliuli, ridge above Kupehau, dry lantana covered slope, June 30, 1935, *Fosberg 10,995;* Honouliuli, Kanehoa Gulch, dry slope, elev. 700 m., Oct. 12, 1927, *Judd 65;* Honouliuli, between Palehua and Palikea, near summit ridge, Dec. 16, 1935, *Degener et al. 11,300;* third small valley northeast of Palikea (contains pipe line arising from tunnel), dry woods, Sept. 19, 1932, *Degener, Park and Bush 7,303* (GH, MICH, NY); north of Puu Pane, sunny gulch at 200 ft. elev., south of ruin of cathedral, March 26, 1950, *Degener and Carroll 20,581* (US); on firebreak trail 1 m. north of Puu Kaua, 1700 ft. alt., on dry slope, Sept. 5, 1952, *Wilson, St. John and St. John 143;* on firebreak trail, 1 m. N. of Puu Kaua, alt. 1700 ft. on dry slope, Feb. 29, 1948, *Cowan 843;* Kahanahaiki, 234 m. alt., dry river bottom, Oct. 16, 1925, *Judd 23;* southern slope of Kahanahaiki Valley, dry forest, Nov. 1, 1931, *Degener et al. 7,296* (GH, MICH, NY); Makua Valley, May 1930, *Russ;* small gulch on south side of upper Makua Valley, dry forest, May 10, 1931, *Degener, Park and Bush 7,295* (GH, NY); Waianae, Feb. 1930, *Meebold 8,629*

(M); U. S. Explor., Exped., highland near Waianae; large branch of Lualualei Valley, southwest of Pohakea Pass, Aug. 4, 1932, *Degener and Bush 7,299* (NY).

No locality: Collect. Dr. Hillebrand, Oahu, Maui (GH).

MOLOKAI: Central Molokai, wet forest, Oct. 13, 1916, *Hitchcock 15,193* (US).

MAUI: Olowalu Valley, May 19, 1920, *Forbes 2417.M* (US); Wailuku, W. Maui, *Hillebrand and Lydgate.*

Eugenia rariflora was first recorded for the Hawaiian Islands by Hillebrand in 1888. It occurs occasionally in the drier regions of the larger islands except Hawaii. This species shows considerable variation in its leaves although not to as great a degree as *E. sandwicensis.*

Both *E. waianensis* and *E. koolauensis* var. *glabra* are here reduced to *Eugenia rariflora* because of intermediate forms which make it impossible to set definite limits upon the two.

The concave leaves would be the only character which would separate *E. koolauensis* var. *glabra* from *E. rariflora.* But a collection from Palikea, Oahu (*Degener 7,303*) has leaves which are only slightly concave; another specimen (*Degener 20,581*) shows leaves that are more strongly concave. This character is certainly not a reliable one, and is of no taxonomic value in this case. This conclusion is supported by the fact that the characters of *E. koolauensis* var. *glabra* are identical in all other respects with those of *E. rariflora.*

The size of the leaves of *E. rariflora* might seem to offer a remarkably valuable taxonomic character, particularly when the extremes in form are considered. *E. waianensis* is described as differing from *E. rariflora* in having smaller leaves. This character seems to be of value when specimens with extremely small leaves are studied (*Degener 7,296*). However, some specimens, such as those collected by Forbes (*2417.M*) and Rock (*17,005*), have leaves which show a series of intermediate sizes between *E. waianensis* and *E. rariflora.* In such cases this character proves to be of little value.

7. **Eugenia koolauensis** Deg., Fl. Hawaii. Fam. 273, 8/10/32.

Tree 4–7 m. tall; branches grey, glabrate, in age the bark reddish-brown, black spotted; leaf scars 1–2 mm. wide, rounded shield-shaped, reddish-brown; leafy branchlets 1–3 mm. in diameter, 4-angled to terete, densely brown subappressed-pilosulous; internodes 9–19 mm. long; leaves 2.5–5 cm. long, 1–3.3 cm. wide, obovate to elliptic, apex obtuse or apiculate, base subcuneate, blade coriaceous, concave, margin entire, more or less strongly revolute, above olive-green, minutely glandular-punctate, glabrous and shiny or subappressed-pilosulous near veins with intervals glabrous, below pale yellowish-green, minutely pitted or pustulate, subappressed-puberulent; midrib shallowly impressed above, elevated below; primary lateral veins, alternate or opposite, 5–7 on a side, 5–10 mm. apart, irregularly ascending at 140–150°, meeting in an irregularly lobed intramarginal vein 1–2 mm. from leaf margin, raised on both surfaces but more distinct below, rarely slightly shallowly impressed above; the veinlets raised-reticulate; petioles 2–4 mm. long, 1 mm. wide, brown subappressed-pilosulous; flowers single or in pairs, axillary; peduncles 1–8 mm. long, subappressed-pilosulous, bracteate; bract subulate, yellow-brown subappressed-pilosulous, 1 mm. long, 1 mm. wide; calyx tube obconic, 2–3 mm. long, 3–4 mm. across, subappressed-pilosulous, subtended by two persistent subulate brown subappressed-pilosulous bracts 1–1.5 mm. long; calyx lobes 4, of unequal length, 1 opposite pair 3–4 mm. long, 3–4 mm. wide, the other pair 2–3 mm. long, 3–4 mm. wide, ovate, green, fleshy, persistent, below finely yellow glandular-punctate, appressed-puberulous, above glabrous, within the tube attached to annular disk; petals 4, white, spreading, persistent, inserted on margin of disk, concave, ovate or obovate or elliptic, apex subacute or obtuse, base truncate, 6–8 mm. long, 4–5 mm. broad, membranaceous, minutely glandular-punctate, ciliate and sparsely puberul-

ous; annular disk raised 0.5 mm. above point of petal insertion, puberulent; stamens numerous (about 150), inserted on disk occupying 0.5 mm. of the marginal region; filaments white, 1.5–5 mm. long, slender, subulate; anthers white, 0.5–1.0 mm. long, orbicular-ovate; style terete, subulate, slightly exserted or included, 2–4 mm. long, sparsely pilose; ovules 8 in a cell, berry ovoid and asymmetric, 1.2–2.0 cm. high, 1.2–1.6 cm. wide, sparingly appressed-pilosulous, light orange-yellow, shiny, minutely yellow glandular-punctate, crowned by the persistent calyx lobes; pericarp fleshy, 1–2 mm. thick; seed globulose, 8–9 mm. in diameter; seed coat thin, membranous, closely adhering to the pericarp and free from the surface of the cotyledons; cotyledons either completely fused or only partly so, or entirely free.

Type: Oahu, "Northern slope of Kaipapau Valley," *Degener and Park 4,169* (BISH).

DISTRIBUTION: Endemic to the island of Oahu.

Specimens examined:

OAHU: Koolau Mts.: Pupukea, dry gulch side, Sept. 28, 1925, *Judd 20;* Pupukea, elev. 300 m., Nov. 2, 1925, *Brown 1, 274;* Kahuku, entrance of Pupukea-Kahuku trail, lower edge of decadent dry forest among lantana, Nov. 22, 1931, *Degener, Park, and Kwon 7,297* (BISH, NY); Laie, Kahawainui Gulch, elev. 100 m., March 2, 1928, *Judd 71;* Hauula, Papali Gulch on trail, March 1933, *Judd;* Hauula, on top of small cliff, elev. 160 m., Sept. 8, 1926, *Judd 54;* Kaipapau, northern slope of Kaipapau Valley, moderately dry woods near top of ridge, Oct. 11, 1931, *Degener and Park 4,169;* Waimea, N. fork of Kamananui stream, very steep, north facing valley wall, alt. 750 ft., April 16, 1949, *St. John 23,683,* and Sept. 5, 1952, *Wilson, St. John and St. John 142,* and Nov. 18, 1952, *Wilson and Lamberton 163;* gully having prominent dyke, north-north-east of Puu Kamaohanui, Dec. 11, 1932, *Degener 7,302* (NY).

Closely related to *Eugenia rariflora*, *E. koolauensis* may be clearly differentiated by its distinctly concave leaves which have subappressed puberulence on the lower laminar surface. It is a rare species and occurs in the rain forest of the Koolau Range on Oahu.

8. ***Eugenia molokaiana*** K. Wilson and J. F. Rock, sp. nov.

Figs. 1 and 2

Arbor 2.5–3 m. alta, ramulis foliosis 0.5–1.5 mm. diametro manifeste tetragonis usque teretibus, crebrissime brunneis subadpressi-pilosulis, internodis 7–24 mm. longis, foliis oppositis 2.0–3.0 cm. longis, 1.4–2.0 cm. latis, suborbicularibus, ellipticis vel obovatis, apice obtuso vel apiculato rare retuso, basi subcuneato, laminis coriaceis concavis, margine integris valde revolutis, supra olivaceis minute pustulatis novellis dense subadpressi-pilosulis, in aetate nitidi-glabrescentibus, subtus pallide flavidi-viridibus minute glandulosi-punctatis dense subadpressi-puberulentibus, petiolis 1–3 mm. longis 1 mm. latis dense brunneis subadpressi-pilosulis, floribus solitariis in bracteorum axillibus, bracteis subulatis dense brunneis subadpressi-pilosulis 1–1.5 mm. longis 1 mm. latis, pedunculis 5–7 mm. longis 0.5 mm. latis subadpressi-pilosulis, calycis tuba 2–3 mm. longa 3–4 mm. diametro subadpressi-pilosula, a 2 bracteis persistentibus subulatis brunneis subadpressi-pilosulis subtensa, bracteis 1.5–2.0 mm. longis, calycis lobis 4 ovatis viridibus carnosis persistentibus longitudine inaequalibus, quorum uno jugo opposito 2 mm. longo 2 mm. lato, altero 3 mm. longo 2 mm. lato, petalis 4 albis in disci annularis margine insertis ovatis vel obovatis 4 mm. longis 3 mm. latis membranaceis ciliatis, apice obtuso, basi truncato vix puberulo minute glandulosi-punctato, pistillo tereti subulato 2–5 mm. longo basi dense puberulenti supra glabroso, stigmati peltato, fructibus ovoideis symmetricibus in sicco 8 mm. diametro dense adpressi-pilosulis rubris insigniter flavidi-glandulari-punctatis calycis lobis persistentibus coronatis.

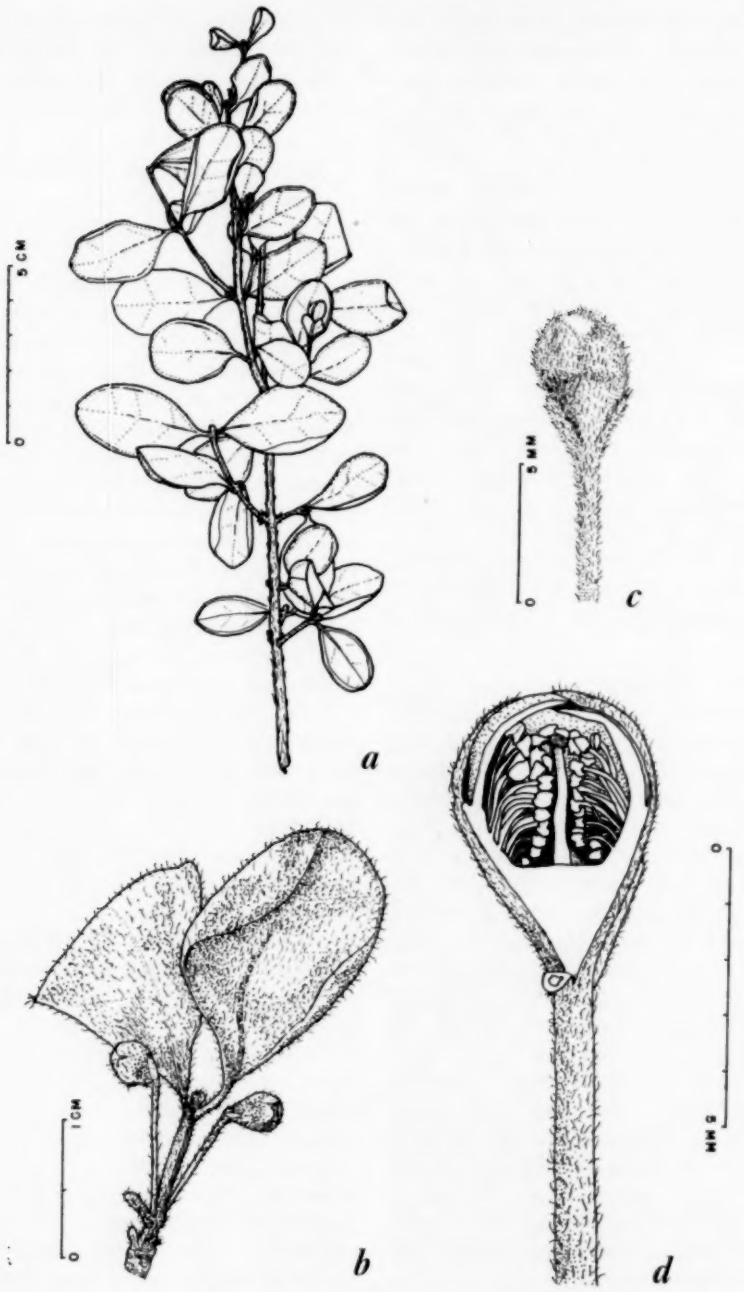

FIG. 1. *Eugenia molokaiana*. *a*, Habit × .50; *b*, flower bearing branchlet × 2; *c*, bud × 4; *d*, dissected flower bud × 8. From Rock 17,144B.

Tree 2.5–3 m. high; branches greyish-brown, glabrate, in age the bark smooth yellowish-red; leaf scars 1–1.5 mm. wide, rounded shield-shaped, reddish-brown; leafy branchlets 0.5–1.5 mm. in diameter distinctly 4-angled to terete, densely brown subappressed-pilosulous; internodes 7–24 mm. long; leaves 2.0–3.0 cm. long, 1.4–2.0 cm. wide, suborbicular, elliptic or obovate; apex obtuse or apiculate, rarely retuse, base subcuneate; blade coriaceous, concave, margin entire, strongly revolute, above olive-green, minutely pustulate, densely subappressed-pilosulous when young, becoming glabrous and shiny in age, below pale yellowish-green, minutely glandular-punctate, densely subappressed-puberulent; midrib shallowly impressed above, elevated below, primary lateral veins alternate or opposite, 5–7 on a side, 4–9 mm. apart, irregularly ascending at 140–150°, meeting in an irregularly lobed intramarginal vein 1.0–1.5 mm. from leaf margin, raised on both surfaces but more distinct below, the veinlets less conspicuous, raised-reticulate; petioles 1–3 mm. long, 1 mm. wide, densely brown subappressed-pilosulous; flowers single, in the axils of bracts; the bracts subulate, densely brown subappressed-pilosulous, 1–1.5 mm. long, 1 mm. wide, peduncles 5–7 mm. long, 0.5 mm. wide, subappressed-pilosulous; calyx tube 2–3 mm. long, 3–4 mm. across, subappressed-pilosulous, subtended by two persistent subulate, brown, subappressed-pilosulous bracts; the bracts 1.5–2.0 mm. long; calyx lobes 4, ovate, green, fleshy, persistent, of unequal length, 1 opposite pair 2 mm. long, 2 mm. wide, the other pair 3 mm. long, 2 mm. wide; petals 4, white, inserted on margin of annular disk, ovate or obovate, 4 mm. long, 3 mm. wide, membranaceous, ciliate, apex obtuse, base truncate, sparsely puberulous, minutely glandular-punctate; stamens numerous (about 150); filaments white, 0.5–2.0 mm. long, slender, subulate, glabrous; anthers white, orbicular-ovate, 0.2–0.5 mm. long; style terete, subulate, 2.5 mm. long, densely puberulent at base, glabrous above; stigma peltate; fruit ovoid, symmetrical, 8 mm. in diameter (when dry), densely appressed-pilosulous, red, conspicously yellow glandular-punctate, crowned by the persistent lobes of the calyx.

Type: Hawaiian Islands, Molokai: Maunaloa; June 1918, *J. F. Rock 17,144*, in the Bernice P. Bishop Museum Herbarium.

Common name: "Nioi."

DISTRIBUTION: Known only from the type locality, Maunaloa, Molokai, and now probably extinct.

Specimens examined:

MOLOKAI: Maunaloa: April 1918, *Rock 17,144;* June 1918, *Rock 17,144;* Feb. 1920, *Rock 17,144B* (BISH, GH).

Eugenia molokaiana is known only from the collections made by Rock at Maunaloa, Molokai. When the locality was first visited in 1918, Rock photographed the tree which was then already dying (Fig. 2). Since 1920 there has not been a single subsequent collection of this species. In 1953 Rock was fortunate in being able to revisit Maunaloa, Molokai, in search of this tree. Unfortunately there is no longer any trace of its existence. *E. molokaiana* has disappeared, like many other trees from that locality.

If ever it should be found, *E. molokaiana* may be easily recognized by its small red fruits, its peltate stigma, and its small, concave, pubescent leaves.

The description of the flower is based on a bud just before anthesis. Unfortunately no open flowers have been seen. The nature of the embryo and seed are not known since it did not seem advisable to dissect the single fruit which was available.

Miss Marie C. Neal informs us that the *nioi* growing on Maunaloa, Molokai, was one of three trees of that region which played an important role in Hawaiian traditions. According to the notes in the Bishop Museum on the native Hawaiian names of plants, the *nioi* from Maunaloa, Molokai, was identified as "the tree form of a god, Kane-ikaulana ula." The tree was used for making images

FIG. 2. *Eugenia molokaiana* growing on Maunaloa, Molokai. (Photo by J. F. Rock.)

by the command of the chiefs, or parts of it were used in "vicious sorcery." The *nioi* growing on Maunaloa was also claimed to be poisonous (Neal, letter). If our identification of this *nioi* as *Eugenia molokaiana* is correct, then we can attribute the belief of its toxicity only to superstition.

TAXA REQUIRING FURTHER STUDY:

Episyzygium oahuense Suesseng. and Ludw., Bot. Staatsaml. München, Mitt. 1: 10, 1950.

The genus *Episyzygium* is based on a single specimen which was collected by A. Meebold in the Waianae mountains in 1930, [A. Meebold 8,445 (M)]. I believe that the peculiar 4-loculed ovary is most likely an abnormality of *Eugenia sandwicensis*. Until such a time that additional corroborative material is collected, I feel that the genus *Episyzygium* and the species *Episyzygium oahuense* should be considered as being based on an aberrant individual.

Hillebrand (1888), Rock (1913), and Degener (1932–34) all reported a rare white form of *Eugenia malaccensis* (*Jambosa malaccensis* f. *cericarpa* Deg.). I have not been able to locate any specimens of this form.

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Origin and Diffusion of the Herzberg Principle with Especial Reference to Hawaii[1]

HAROLD S. PALMER[2]

WHEN IT BECAME KNOWN in Hawaii that successful artesian wells had been sunk in many parts of California, various people discussed the question whether artesian water existed in Hawaii. Certain optimists brought a capable well driller from California in 1876, but were emphatically rebuffed when they sought financial help from the government. According to H. M. Whitney (1898), the decision lay with the Finance Minister, who refused money for a test well because he held that all "caverns" below sea level were filled with salt water, and that any rain water reaching the caverns became salt water at once. How wrong he was appeared just three years later when James Campbell, at his own expense, had a good well drilled in Honouliuli.

As more wells were drilled, it was learned that holes near the sea or near the axes of valleys were apt to be failures. We have no evidence as to how well the hydrologic conditions were understood. In 1882 Judge McCully described the successes to that date. Appended to his article is some material by an unnamed writer, who thought correctly that the fresh water was prevented from escaping to the sea by impervious strata, which he called "very compact clay." This, certainly, is a very important factor in the modern explanation of the artesian conditions in Honolulu.

Schuyler and Allardt concluded in 1889 that the Pearl Harbor Springs and the artesian wells drew from the same source of supply, as shown by the fact that water rose in the artesian wells only a little higher than the highest springs. They wrote, "The probabilities are that the island is surrounded by deep thick strata of impervious clay . . . , that these strata lap onto the land to the height the water rises in wells, . . . and that these strata prevent the escape of the waters into the sea beneath them." They seem to be the first to point out the relation between the height of what we now call "cap rock," and the artesian level. A diagrammatic cross section illustrates their views to some degree. Unfortunately their report was a private affair and was not widely circulated, one supposes, so that their understanding of the extensive "basal ground water body," as we now call it, was not utilized by others.

In 1875, Franklin C. Hill told how good water could be gotten by digging shallow wells in sand islands off the Gulf Coasts of Mississippi and western Florida. He explained the presence of fresh water by analogy to an "ash leach," a vessel, such as a barrel, tight enough to hold wood ashes but with small openings at the bottom through which liquids could escape. Hot water poured in on top of the wood ashes leaches out potassium salts, sinks downward and out at the bottom. As more and more water is added it drives the previous lots of water downward with little mixing. Hill draws a parallel with water from rain driving salt water down to some depth

[1] The Herzberg principle holds that in oceanic islands and along shores of larger land masses fresh water floats on and is underlain by sea water because of their differences in density.

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on sand islands making what he called a "lake of fresh water held by the sand in the midst of the sea." He shows that with a porosity of one-third, a 12-foot layer of sand is equivalent to a lake 4 feet deep, and that an acre would hold about one and a quarter million gallons. He seems not to have considered the relative densities of fresh and salt water or of pure water and water holding potassium salts in solution.

In the next decade much progress was made in Europe. In 1888–89, W. Badon Ghyben, a Captain of Engineers in the Netherlands Army, as a result of studies near Amsterdam, found fresh water under the coastal dunes and resting on salt water, and observed that the depth to the salt water increased inland from the shore. He assumed that the specific gravity of North Sea water was 1.0238, from which he calculated that the depth below sea level to salt water was about 42 times the height of fresh water above sea level (1.000/0.0238 = 42.01).

A better exposition of the idea was published by Alexander Herzberg in 1901, based on studies on the island of Norderney. A hole was drilled near the middle of the island to learn about its geologic structure. Cox's translation reads, "It could not be doubted after these observations that the fresh water floated on the subterranean salt water." In another place we read, "The deep position of the sea-water boundary is a function of the height of the ground water table in the dunes above mean tide level in the sea." Herzberg used 1.027 as the specific gravity of North Sea water and from it calculated that the sea water boundary was 37 times as far below sea level as the water table was above sea level. Although Herzberg did not publish until 1901, he seems clearly to have made use of the principle as early as 1889, or even 1886, in his work as a consulting hydrologic engineer.

After Herzberg's publication, there was much discussion of the details of the principle by Dutch, Belgian, French, and German workers.

According to Watson (1956), the early Hawaiians had gotten water from small, shallow wells dug near the shore. Between 1894 and 1900 Maui plantations made thirteen large-scale basal water developments which were gigantic forms of the shallow wells of the early Hawaiians. These were large pits sunk from ground heights of 20 to 50 feet, and large volumes of water were pumped by great steam pumps. These installations had two bad features. For one thing the water was rather saline because the fresh water lens was thin in the absence of a cap rock. Secondly, a very long pipe line was needed to carry the water to the cane fields.

In 1899, Henry Perrine Baldwin and his consulting engineer, Herman F. A. Schussler, believed that fresh water extended far inland under central Maui, as what we now call the "basal ground water body." A shaft (H. C. & S. Co.'s "Kihei," No. 3) was sunk about three miles from the shore from a height of 303 feet. The shaft was 323 feet deep and the water table was 6 feet above sea level. Skimming tunnels were driven close to sea level and a large supply of irrigation water was obtained. This was the first "Maui-type basal water development," and has been followed in Hawaii by more than 50 others of the same general type.

Thus it is clear that in the Hawaiian sugar industry the existence of the great basal ground water body was known, even though it had not been satisfactorily explained.

Waldemar Lindgren spent part of 1901 on Molokai, and wrote (1903):

> In the absence of any impermeable stratum or basins filled by clayey materials, such as, for instance, exist on Oahu, there is nothing to prevent the sea water from entering the rocks freely and assuming a level differing but little from sea level. Below a certain level there is no reason to expect anything but sea water.
>
> On the other hand, the rain water also sinks freely through the porous rocks until it meets the sea water. Here, at the permanent water level it is held by the counter pressure of the sea water, and in fact rests like a sheet upon the

same. Between the underlying salt water and the fresh water on top of it there is an intermediate zone of varying width in which the two mingle to form brackish water. The fresh water, always receiving additions from above, is slowly but steadily moving to the only outlet it can find —that is, to springs located along the sea shore, just above or a little below sea level.

The surface of the salt water "is . . . about 160 feet below the surface of the ground [near the south shore]. Inland this level sinks. . . . The permanent surface of fresh water rises inland very slowly, so that a mile or more inland the water in wells may stand only a foot or two above sea level."

Attention is called to Dr. Lindgren's reference to the "counter pressure of sea water," and to his observation that the water table rose inland and that the salt-fresh boundary dropped inland. He was very close to developing the idea of the fresh water lens.

In the following years a number of studies were made by members of the U. S. Geological Survey in states bordering the Atlantic and Gulf Coasts.

Harris in 1904 held that fluctuations of water levels in wells in Louisiana were responses to loading and unloading of impermeable strata over the water-bearing strata by tides and by strong onshore winds. Also, that the fluctuations did not depend on any direct connection between the water of the Gulf and the water in the artesian aquifers.

Pennink in 1904 discussed before the International Engineering Congress in St. Louis some of the features of the relationship between fresh and salt water under coasts and islands, based on his work in the Netherlands. Unfortunately the title of the paper (1905) did not reveal this topic, so that it did not come to the attention of geologists. It is not nearly as forthright a presentation of the Herzberg principle as one would wish.

Veatch and others (1906), in a big report on the ground waters of Long Island, N. Y., made no reference to any possible relationship between fresh and salt water. Twelve north-south profiles of the island and its water table have as their bases the line 20 feet below sea level. Curiously these profiles have the pattern for the saturated zone extend out under both the north and south shores, as if fresh water extended under the waters of the bays at the south and those of Long Island Sound on the north. It would seem, therefore, that they gave no consideration to the effect of salt water.

Veatch in 1906, in a smaller paper, wrote that the water level under Long Island coincided with sea level at the shores and became higher inland, but said nothing about any underlying salt water.

Taylor, writing in 1907 of the salinity of some wells in the Texas Coastal Plain, offered no explanation of the salinity.

We now come back to Hawaii again, for in 1908 W. D. Alexander discussed the ideas ascribed to McCully and wrote that McCully (really some unnamed person) held that "it seems evident that the great central stratum of water-bearing rock must be completely surrounded by impervious strata from the surrounding ocean. Were it not so, the water it contains would escape into the sea instead of standing at forty-two feet above it." Alexander agreed with most of these ideas, but not entirely, for he wrote, "On the whole the theory . . . seems . . . to be the most probable one, although it may not be necessary to assume that the 'water-bearing rock must be completely separated by impervious strata from the ocean,' in view of the slowness with which water percolates through rock and gravel, and also of the pressure of the sea water." Unfortunately Alexander did not develop the germ of the idea further, perhaps because not more than 23 well logs could have been available to him then.

It remained for Andrews, in 1909, to make a tremendous advance in the understanding of the artesian system at Honolulu. Like McCully's ghost writer and Alexander, he thought the barrier of "clay" played an important role, but he developed the all-important part played

by the balance between salt and fresh water. He wrote, "The water-bearing stratum is the lava of the volcanic dome as it was finally completed by the upbuilding volcanic forces. The water-bearing lava rock is covered with a layer of clay, the product of decomposition of lava, which in turn, is covered with a stratum of coral rock, formed as a fringing reef, above which strata of coral and volcanic material may alternate. The depth below sea level to which the retaining clay stratum would need to extend in order that fresh water in wells should be raised forty-two feet above sea level by the hydrostatic pressure of sea water of density 1.026, is 1614 feet, which is but little deeper than the depths at which clay was found in the deeper wells." (The 1.026 specific gravity for sea water would give a ratio of 38.5 between the depth to sea water and the height of fresh water: 1.000/0.026 = 38.46.)

"An arrangement of coral and clay strata such as here presented fully accounts for the phenomenon of flowing wells on an island of volcanic origin. The lava of the volcanic dome is somewhat porous, penetrated by cracks, and open enough to permit the movement of water; the clay stratum overlying the lava prevents the escape of water upward; the remaining coral and clay strata simply add an overlying mass, and the elevation of the uppermost coral layer above sea level, lined as it is by clay, raises the surface of the underground water accumulations until they escape as springs over the coral brim, or rise above sea level in artesian wells to the height of escape."

Thus it appears clear that Andrews, who had no knowledge of the work done in Europe on coastal ground waters, entirely independently worked out what we now call the "Herzberg Principle." On Dec. 24, 1955, I called on Professor Andrews and we discussed the matter at some length. Apropos of statements sometimes made that Andrews got his ideas from the Alexanders (plural), he told me that Arthur C. Alexander merely transmitted his father's idea that sea water exerted a pressure. Working out mathematically the ratio of the depth to salt water to the height of the water table, as a function of the relative densities of the two liquids was entirely Andrews' idea. Thus Professor Andrews seems clearly to be the first American to give a mathematical expression of the ratio.

Andrews' remarkable insight into the phenomena is also shown by his correctly explaining the so-called "clay," which acts as the restraining member, as the impermeable residual matter due to very advanced weathering in place of the upper or outer parts of the body of lavas. Others had thought that the clay originated as some sort of marine sediment at a time when the sea reached higher on the island. It is hard to think that clay, in water, would remain in place on steep submarine slopes.

It is most unfortunate that Andrews' paper was never printed, for in its typescript form it gained only moderate circulation.

In 1908 Gregory and Ellis described fluctuations of water levels in wells near the Connecticut shore, but did not refer to the density of sea water. They reported one well in Norwalk that had fresh water to a depth of 50 or 60 feet in sand, but only salt water at lower levels. Plugging of the bottom of the well shut off the salt water successfully.

Clapp, also in 1909, reported on conditions in southern Maine, where salt water had been found under fresh water in a good many wells near the shore, but he made no mention of the density of sea water. A typical well in Islesboro, "obtained good water at 181 feet from the surface, but drilling continued, and at 220 feet salt water was encountered. The well was filled with Portland cement to a depth of about 200 feet from the top, the sea water being thus shut off, and the water was reported of good quality in 1906."

Hitchcock, in 1910, in an address to a Special Conservation Meeting held in Iolani Palace, told of the lava rock aquifer and the cap rock of the artesian system. He made some use of Alexander's idea of the pressure

of sea water, but made no reference to Andrews' thorough and invaluable development of that idea. This omission by Hitchcock may be taken to illustrate the unfortunately limited circulation of Andrews' paper.

We next go back to Long Island, where Spear in 1912 applied the Herzberg principle, I think for the first time in any American ground water study. He mentions some of the studies made in Europe, and gives a diagrammatic cross section of the lens under a simple island. He shows the derivation of the "40 to 1" ratio where the specific gravity of sea water is 1.025, and also other ratios for other densities of sea water. A diagrammatic cross section of Long Island is given, in which the base of the fresh water lens is truncated by a smooth basement of impermeable rock instead of making the full downward curve. The principle was used by Spear in forecasting the behavior of wells in certain localities.

Unfortunately for geologists, Spear's work was published in an engineering report for the New York Board of Water Supply, which few geologists would be apt to read.

In 1912 the first edition of Keilhack's "Lehrbuch der Grundwasser- und Quellenkunde" was published. It was followed in 1917 by an enlarged and revised edition, pages 162 to 165 of which give an excellent presentation of the work of Badon Ghyben and Herzberg, and others. One cross section shows the conditions in an ideal, symmetrical, homogeneous, permeable, and rainy oceanic island. The University of Hawaii Library received a copy of the second edition as early as 1921, but it has been little used.

Matson and Sanford in 1913 came close to the idea of a lens of fresh water under Florida. Florida, of course, differs greatly from Hawaii in its rock types, structure, shifts relative to sea level, and its hydrology.

One earlier geologist had thought that the fact of finding fresh water in marine limestones to a depth of a thousand feet implied a former uplift of Florida by a thousand feet, but Matson and Sanford pointed out that the uplift need not have been more than enough to give a small hydrostatic pressure. Thus, they had come close to the Herzberg principle, as is also shown by the following quotations.

> The rocks of Florida are all sedimentary and for the most part were deposited beneath the ocean. Such deposits are called marine and originally included sea water, which may be called water of deposition. This included sea water may be gradually displaced by descending rain water—the rate of change depending on the freedom of drainage. Where the rocks are porous and the land high the water of deposition is soon removed, but a low altitude combined with dense rocks gives a very slow rate of escape. The process of removal may extend to some distance below sea level provided porous materials emerge on the bottom of the ocean. The exact depth will be controlled by the relative weights of the columns of fresh water beneath the land and the salt water at the point of emergence.
>
> The greater height of the column of fresh water is partly offset by the increase of weight of the sea water caused by its high mineral content and by the friction of the water in the rocks. There must inevitably be a level where the opposing forces counterbalance each other and the underground water becomes nearly static. Below this level the water of deposition is scarcely disturbed.

This was certainly an approach toward the Herzberg principle.

A well at Sumterville, far from the shore, found no salt water though it reached a total depth of nearly 2,000 feet.

Another quotation from Matson and Sanford makes an approach to the idea of a lenticular body of fresh water, and is as follows:

"In passing from the interior of the State toward the coast the depth to salt water diminishes until in many places it may be encountered within less than 500 feet of the surface, though the depth to the strong brines is usually somewhat greater." This passage suggests the downward curve of the lower side of an ideal lens, but does not mention

the corresponding upward curve of the water table or top of the lens.

In 1916 Palmer (1920) thought that the gneiss of Long Neck Point, in Darien, Connecticut, had important joints striking about north and south, parallel to the length of the peninsula, and dipping steeply westward. Wells drilled on the west side of the peninsula got fresh water, but those on the east side got only salt water, which was presumably led into them from the Sound by the westward dipping joints.

In the fall of 1919, Palmer (1919) studied the ground waters of Peaks Island in the harbor of Portland, Maine. The island of 800 acres has a discontinuous mantle of glacial till over schists, whose joints are the main source of ground water. The seven drilled wells on the island extended 3, 105, 110, 110, 146, 166 and 276 feet, respectively, below sea level. The chloride contents of the waters of only five were determined and ranged from 17 to 21 parts per million of water. A slight approach to the Herzberg principle is indicated by the following passage, "The zone of active circulation on Peaks Island is probably entirely above sea level except where it is stimulated by the draft of deep wells. There is probably a more or less conical body of fresh water underlying the island, the point of the cone downwards. The limit of this cone is determined by a balance between fresh water originating on the island and the salt water trying to work under the island." From a 1956 point of view it would have been better to have referred to a "conical region in which the joints contain fresh water," and still better to have used "dome" or "bowl" instead of "cone."

A typescript report by Palmer in 1921 for the Bernice P. Bishop Estate dealt with Maunalua, Oahu. This considered the restraining effect of cap rock where it is present, but made no reference to the density of sea water.

In 1919 the field work of Brown, on the relation of sea water to ground water along coasts, led to two papers that are important landmarks in our story. In a first, smaller paper Brown (1922) introduced to American geologists the work of Badon Ghyben and especially that of Herzberg. Besides giving the formulas and their derivation he reproduces Herzberg's cross section of Norderney and also gives diagrammatic sections of the conditions under an ideal, permeable island and along a permeable coast. There is also reproduced a cross section from a Dutch paper by Pennink of a dune ridge on the Holland coast with isochlors outlining the somewhat lenticular body of fresh ground water.

In the fall of 1955 I wrote Dr. Brown asking how he came across the writings of the European workers. His reply was, "As I recall, I deliberately instituted a search of literature in the Library of Congress on Holland's water problems, on the hunch that that should provide illuminating data, due to the coastal dune belt. This led me on to Badon Ghyben. Somewhere later . . . I ran across a reference to Herzberg."

In 1923, Meinzer's *The Occurrence of Ground Water in the United States* was published. This makes no reference to the Herzberg principle. In one place it points out that, where ground water is found in joints, there is more danger of salt invasion if joints dip landward than if they dip seaward. In another place, apropos of the water-bearing Tertiary strata of the Coastal Plains, we read, "Their water is generally good in the areas of outcrop and for some distance down the dip but is likely to become salty where the formations pass to considerable depths in the direction of the sea."

About 1924, Dr. H. L. Lyon (1925) used the ratio of 1.000 to 1.024 for the densities of normal Honolulu artesian water and sea water, in estimating the reduction of our original supply of fresh underground water. This is in the first part of a typescript, the last part of which was published on Jan. 1, 1925, along with the paper referred to next below.

Carson, McCombs and Rothwell (1925) made a report on the artesian wells of Hono-

lulu, and used Dr. Lyon's density ratio. They estimated that the fall in head to 1925 implied that over 50 per cent of the amount of water originally stored underground had been removed. Though they did not use the term, either they or Dr. Lyon seem to have been the first to hit on the idea of "bottom storage."

A report on the ground waters of the island of Lanai by Palmer (1924) includes a diagrammatic cross section of the water table in an ideal, symmetrical, homogeneous, permeable, and rainy island, showing the upward curve, but it does not have the corresponding downward curve of the base of the fresh water body. Apparently Brown's first paper had been forgotten. Wentworth (1925), in his larger report on Lanai, seems to have been misled by Palmer's erroneous, incomplete cross section.

Another great landmark was Brown's larger paper, published in 1925 though also based on his 1919 field work and subsequent office and library work. It adds little for the present purpose, but it surely had a different and more extensive readership than did the earlier, shorter paper. It has formed the basis for subsequent work on ground waters in Hawaii and many other regions. It includes an annotated bibliography of relevant papers.

One important effect of it may be found published in the abstract of Palmer's paper presented May 19, 1926, before the Hawaiian Academy of Science, namely the use of the "U-tube" analogy for illustrating the balance between salt and fresh water.

A fuller paper resulted from the preceding, and was published in October 1926. So far as appears, it presents the first deductive explanation of the artesian conditions at Honolulu, by the use of three progressively more complex cross sections of ideal, oceanic islands. The first is a symmetrical, homogeneous, permeable, but rainless island, in which sea water fills all the voids below sea level. The second adds an effective amount of rain that eventually supplies fresh water to a lens floating on denser sea water. In discussing this cross section the algebraic derivation of the Herzberg ratio, 40 : 1, is given. The third cross section adds an impermeable coastal capping that thickens the edge of the freshwater lens so as to cause artesian conditions. Combined in this are the three essential factors: (1) the permeable lava rock aquifer; (2) the impermeable coastal plain cap rock; and (3) the Herzberg principle.

On Sept. 10, 1926, Palmer transmitted to the Honolulu Sewer and Water Commission his report on the Honolulu artesian system (1927). The ideas of the paper discussed just above were included and somewhat expanded. This report made several contributions. One was the explanation of the differences in the heads of the several isopiestic areas as a result of their being partly separated by deep valley fills that acted as inverted, underground dams. Another idea, thought to have been new then, was that of ascribing the gradation downward from fresh through brackish to salt water in the "contact zone" to mixing as a result of rise and fall of the contact zone in response to falling and rising artesian heads. With falling head, the contact zone would rise bringing saltier water where fresher water had been; and with rising head, the contact zone would drop and bring fresher water where saltier water had been.

There was also the first, though inadequate, attempt to study the rate of change in the "transition zone," as we now prefer to call the "contact zone." Studies of the reduction of salinity in two wells by plugging parts of the bottoms, gave changes per foot of plug of 1.75 parts and of 25 parts of chloride per million parts of water. The slow rate of change in the first well was thought to be due to greater fluctuations of the depth to the transition zone as a result of greater fluctuations of the artesian head, with more mixing as a result.

From 1926 on there have been many applications of the Herzberg principle, not only at various places in the Hawaiian Islands, but also on many Pacific islands, especially during World War II. There has also been application

of the principle, with certain necessary modifications, to the stratified sedimentary rocks of the Atlantic and Gulf Coastal Plains, and to the limestones of Florida, as well as to the glacial deposits of Long Island.

In Hawaii, Dr. Chester K. Wentworth, when he was with the Honolulu Board of Water Supply, made important studies of the specific gravity of sea water in connection with the local value of the Herzberg ratio, of bottom storage, of the growth of the transition zone; and of modifications of the Herzberg principle by taking a dynamic instead of the original static view. Mr. L. T. Bryson, Chemist of the Board of Water Supply, has studied, among other things, base exchange in Honolulu ground waters and the nature of the transition zone. Mr. Doak C. Cox, Geologist for the Hawaiian Sugar Planters' Association, has made great progress in studies of the transition zone, of the effects of ocean tides on ground water levels, and of the dynamic *vs.* static view of the Herzberg principle.

I am indebted to Mr. Doak C. Cox, Mr. Leslie J. Watson, and Mr. Erik Palmer for critical reading of the draft of this paper and for their valuable comments.

EPILOGUE

Some years ago we spoke of just the "Herzberg Principle." Then, when it was realized that Badon Ghyben published first, we spoke of the "Ghyben-Herzberg Principle." Next it was learned that the Hollander's family name was double, viz., Badon Ghyben, so it was felt that we should say the "Badon Ghyben-Herzberg Principle." I now propose that we return to the simple form of "Herzberg Principle," with its various parallels, such as "Herzberg Lens." I believe this is justified, although Badon Ghyben published first, because Herzberg (1) had the idea first and used it, and (2) gave a far better presentation of the idea.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part II. Collection from Arno Atoll, Marshall Islands[1]

ALBERT H. BANNER[2]

THIS PAPER reports upon a collection of snapping shrimp made by Dr. Robert W. Hiatt and Dr. Donald W. Strasburg, of the University of Hawaii, at Arno Atoll in the southern portion of the Radak chain of the Marshall Islands. Under the sponsorship of the Pacific Science Board with funds from the Office of Naval Research, they visited Arno during the summer of 1950 as a part of a scientific team to investigate the total ecology of the atoll. One additional shrimp reported upon was collected by Dr. J. W. Wells of the same investigation.

This study of the snapping shrimp from Arno was initiated under a grant administered by the U. S. National Museum and the Pacific Science Board under a contract between the Office of Naval Research, Biology Branch, and the National Academy of Sciences, (NR 160–175); some help in the final phases of the study was made available through a grant to the author from the National Science Foundation (NSF-G-1754).

To avoid repititious synonymies and bibliographies in this series of papers, whenever a full citation for a species has been given in an earlier paper, by myself, reference is made to this citation. In this present paper reference is made only to Part I of these studies, describing collections from the Mariana Archipelago (Banner, 1956). Type specimens for the new species described in this paper will be deposited in the United States National Museum.

ARNO ATOLL

The nature and biology of Arno Atoll has been covered in a series of preliminary reports by members of the investigation team, published (in mimeographed form) in the *Atoll Research Bulletin* (issued by the Pacific Science Board), Numbers 3–11, 1951–1952. A comprehensive book on these studies is now in preparation and specialized scientific reports are appearing in technical journals.

Arno is an irregularly shaped atoll centered about 7° 05′ N., 17° 40′ E. and about 27 miles across its longest axis (Fig. 1). It consists of 133 islands and islets, only a few of which are large enough to support human habitation. The outer margin of the atoll drops off steeply into waters of profound depth; within, the lagoon is estimated to be 100–200 feet deep. The ocean communicates with the lagoon through a series of passes, deep or shallow. The atoll lies in the belt of northeasterly trades and at the southern edge of the North Equatorial Current, which may be replaced during some of the months of northern summer by the Equatorial Countercurrent. The ring of islands is surrounded on both inner and outer margins by coral reefs of varying vitality and breadth, depending upon conditions of wind, surf, sediment, etc.

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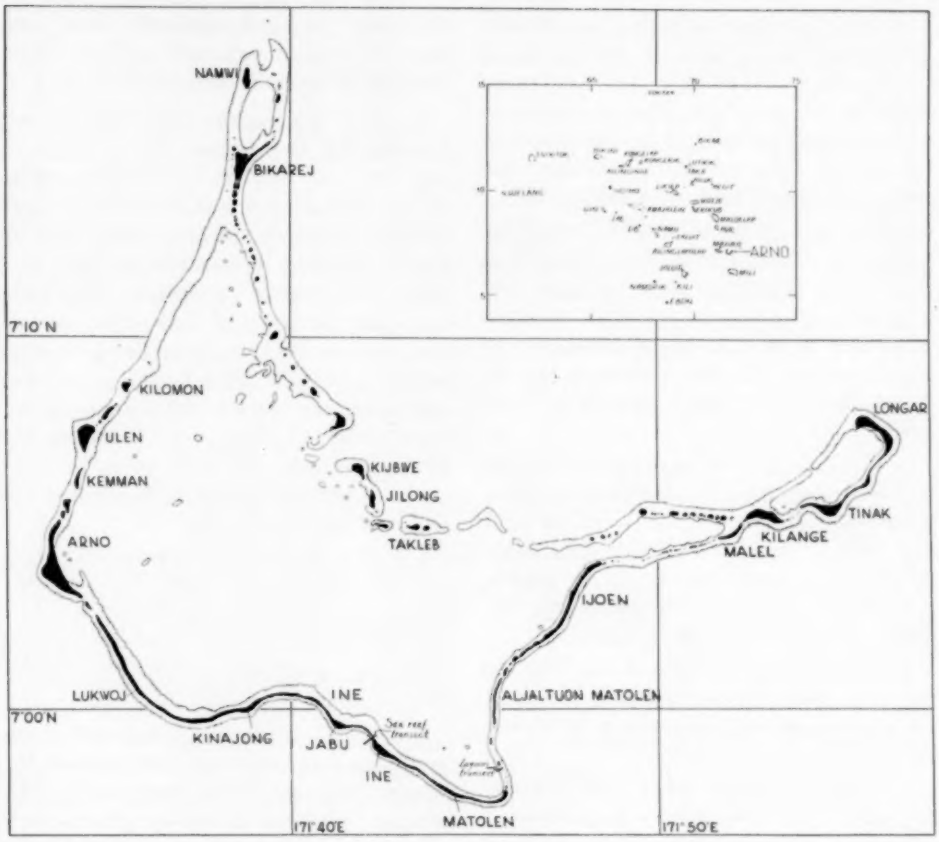

FIG. 1. Map of Arno Atoll, showing collecting stations. *Insert*: A map of the Marshall Islands, showing the location of Arno.

HABITATS OF THE SHRIMP

The studies made by Dr. Hiatt include two ecological sections of the reef in the extreme southern section of the atoll, one on the seaward and one on the lagoon side. The study of the seaward reef was made near the village of Ine, in a region quite protected from the prevailing winds and surf; that of the lagoon reef was made off the islet of Makīn, some 4 miles away.

The method of taking the transects was the same in both cases. A strip 50 feet wide and divided into sections, 50 feet long on the seaward reef and 100 feet long on the lagoon reef, was laid out normal to the shore and running from the beach to water beyond "skin diving" depth. The animals in each section were collected, given field identification and preserved; in the shallow zones this was done by wading, in the deeper by "skin diving."

The contours found on both transects were about the same, showing a broad, relatively flat, gradually sloping reef centering about the height of mean low water. An abrupt change in slope marked the outer margins of the reef flat, with the slope becoming steep on the lagoon reef and precipitous on the ocean side.

A complete report on the ecological study is in preparation by Dr. Hiatt. For this report on a small section of his collections, loaned to me for this study, Dr. Hiatt has permitted me to extract and summarize the following information from his field notes about the zones and specific habitats of the shrimp:

E–1–2. Section XI, seaward reef. Slope beyond edge of reef flat, about 450 feet from shore. Reef face at an angle of about 60°. 82 species of coral collected down to depth of 30 feet, no species being dominant. Alpheids commensal with *Antedon*, a sea lily found clinging to the underside of coral ledges.

E–1–106. Section III, seaward reef. 50–100 feet from beach. Level about that of mean low water (0.0); on low tides area with dry areas and shallow pools. Corals not flourishing, *Montipora gaimardi* the dominant species. Sand and coral fragments in depressions. Alpheids in interstices of *M. gaimardi*.

E–1–122. Section IV, seaward reef. 100–150 feet from beach. In general similar to Section III, about same level. Alpheids as in Section III.

E–1–149. Section V, seaward reef. 150–200 feet from beach. Inner portion alone exposed on extreme low water, outer portions covered by 2–5 inches of water. Level of extreme low water marks division between *M. gaimardi* and *Acropora pectinata* zones. Alpheids as in Section III.

E–1–285, 290. Section VI, seaward reef. 200–250 feet from beach. Water standing at all tides, reef flat bare with no loose sand. Zone with mixed *M. gaimardi* and *A. pectinata*. Alpheids in group 285 collected from living heads of coral and in holes in dead coral, and in group 290 from living heads of *Pocillopora*.

E–1–305. Collected from a brackish pond on Malel Island.

E–1–306. Section VII, seaward reef. 250–300 feet from shore. At tides below 0.3, tips of growing heads of coral exposed. *A. pectinata* dominant coral, covering much of area; *Pocillopora* luxuriant. Alpheids from dead bases and living branches of coral; some from living heads of *Pocillopora*.

E–1–387, 388. Section VIII, seaward reef. 300–350 feet from shore. Highest parts of corals exposed only on extreme low waters. *A. pectinata* dominant with *Pocillopora* secondary; a brown alcyonarian, *Lobularia krempfi*, also occurring in numbers. Alpheids collected from heads of *Acropora* and *Pocillopora*.

E–1–611, 630, 643, 648. Section IX, seaward reef. 350–400 feet from shore. Section similar to Section VIII, the depth slightly greater and area commonly flooded with foam from surf much of day. *A. pectinata* and *Pocillopora* still dominant corals. Alpheids collected from heads of *Acropora* (617,643), *Pocillopora* (619, 630), and *Stylophora* (648).

E–1–670. Section II, seaward reef. From edge of water at mean high tide to a point 80 feet seaward. Exposed beachrock pitted and covered with fine, short algae; area marked by large tide pools varying from 4 to 8 inches deep. Alpheids collected from tide pool.

E–2–169, 311. Section II, lagoon reef. From mean high tide level to 100 feet towards the lagoon. Outer margin uncovers at 0.0 tide. Covered with quite smooth beachrock, with a few shallow tide pools; outer portions covered by a fine sand veneer. No corals present. Alpheids collected under loose slabs of beachrock (169) and in holes in the rock (311).

E–2–343, 382. Section IV, lagoon reef. From 200–300 feet from shore, depth from 4 to approximately 60 feet. Area with bottom covered with sand and coral rubble, and numerous species of coral with those of the genus *Acropora* dominant. Alpheids collected from heads of *Seriatopora hystrix* (343) and *Stylophora* (382).

E–2–360. Section III, lagoon reef. From 100–200 feet from shore. Depth from 0.0 to 4 feet. Section of bottom covered with fine sand and coral rubble; luxuriant growth of corals with species of *Acropora* dominant. Alpheids collected from *Stylophora mordax*.

ATHANAS Leach

Athanas djiboutensis Coutière, 1897

For synonymy, see Banner, 1956.

LOCALITIES: One specimen each at E–1–290 and E–1–388.

DISCUSSION: The two specimens cannot be assigned positively to this species for they are both fragmentary, lacking their chela and some other appendages. However, the appendages still remaining, and especially the form of the rostrum and the orbital spines about the eyes, compare almost perfectly with the specimens from Saipan identified as this species.

Athanas marshallensis Chace
Fig. 2

Athanas marshallensis Chace, U. S. Natl. Mus., Proc. 105(3349): 17, fig. 8, 1955.

LOCALITIES: One non-ovigerous female from E–1–122.

DISCUSSION: This specimen differs in only one way from the description and figure of Chace: in this specimen the extracorneal spines reach almost to the anterior margin of the eyes, instead of midway along the eyes as in Chace's specimens. It is likely, however, that the eyes are rotated backwards towards the body, for the "collar" of the anterior carapace that usually fits snugly about the eyes is loose and stands out from the corneas in this specimen.

METABETAEUS Borradaile

Metabetaeus minutus (Whitelegge)

Betaeus minutus Whitelegge, Austral. Mus., Mem. 3: 147, pl. 7, fig. 4, 1897.

Metabetaeus minutus Borradaile, Zool. Soc. London, Proc. 66: 1014, 1898.

Metabetaeus minutus Coutière, Soc. Ent. de France, Bul. 1899(19): 374, 1899a.

LOCALITIES: Four specimens, all females without eggs, maximum length 17 mm., E–1–305.

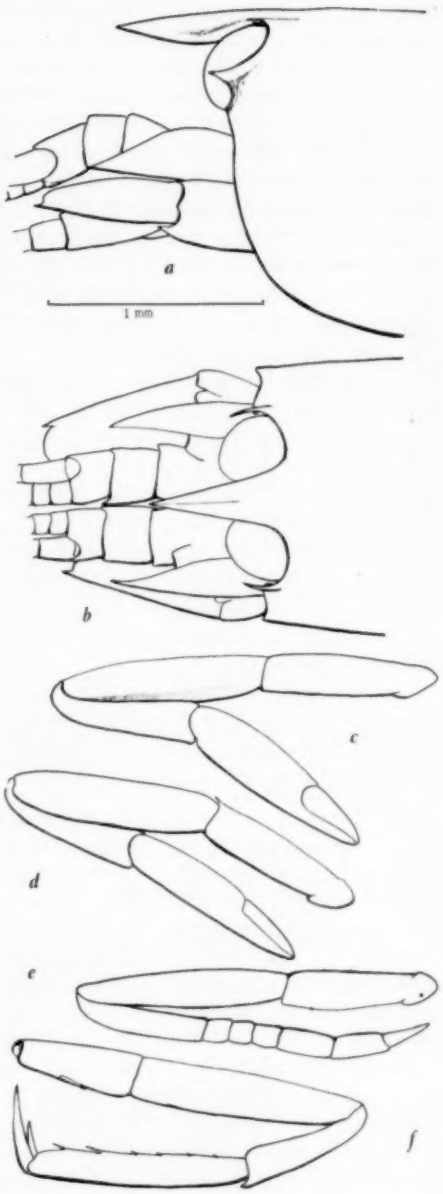

FIG. 2. *Athanas marshallensis* Chace. *a*, *b*, Anterior body region; *c*, right cheliped; *d*, left cheliped; *e*, second leg; *f*, third leg. (All same scale.)

DISCUSSION: These specimens agree almost perfectly with Whitelegge's original description and with the later redescriptions. The only differences found are in the anterior body region when compared to the plate of the original description. In these specimens the rostrum is almost an equilateral triangle with straight sides and slightly rounded tip, while Whitelegge showed and described his specimen as having a slightly more narrow rostrum with concave sides and an acute tip. Further, the concavity between the base of the rostrum and the orbital spines is more pronounced. Finally a difference is found on the relative lengths of the antennular and antennal peduncles, for in these specimens the antennular peduncle is slightly longer than the antennal, rather than the reverse as described by Whitelegge. These differences are minor and most likely of no importance.

Otherwise the specimens agree in the general form, the proportions of the appendages, the branchial formula and even in the possession of a brown spot on *corpus mandibulae* described by Coutière.

The type specimens came from a mangrove swamp, and, previous to this report, were the only specimens known. The ones described from Arno came from a brackish pond.

SYNALPHEUS Spence Bate

Comatularum Group

Synalpheus carinatus (de Man)

Alpheus carinatus de Man, Arch. f. Naturgesch., 53: 508, pl. 22, fig. 2, 1887.
Synalpheus carinatus de Man, Siboga Exped. 39a¹(2): 210, pl. 5, fig. 23, 1911.
nec Synalpheus carinatus Pearson, Report on Pearl Oyster Fisheries, p. 83, pl. 2, fig. 9, 1905.

LOCALITIES: One specimen at E–1–2, (commensal with *Antedon*, a sea lily).

DISCUSSION: This specimen agrees perfectly with the characteristics given by de Man. The ova are 1.1 by 0.7 mm. The species will be discussed more fully in a later paper. Hiatt notes that the color in life was brownish-black, the same as the host, *Antedon*.

Synalpheus consobrinus de Man

Synalpheus consobrinus de Man, Nederland. Dierk. Ver., Tijdschr. II, 11: 111, 1909.
Synalpheus consobrinus de Man, Siboga Exped., 39a¹(2): 204, pl. 6, fig. 21, 1911.

LOCALITIES: One specimen at E–1–643.

Neomeris Group

Synalpheus charon charon (Heller)
Fig. 3

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens each at E–1–617 and E–1–630.

DISCUSSION: These four specimens are of the parent subspecies with the expanded base to the superior unguis of the third to fifth legs, and with a rostrum of uniform taper.

One specimen from E–1–617, however, had a greatly expanded palm of the large chela with greatly reduced fingers. The condition is slightly more pronounced than that found in *S. macromanus* Edmondson (1925: 9), and at first the specimen was tentatively identified as that species. But *S. macromanus* has a conical inferior unguis on the third leg and is otherwise similar to *S. paraneomeris* Coutière, while this specimen is identical to *S. charon* except for the form of the large and small chelae.

The question is how this enlargement of the chela should be interpreted. When there was but the one specimen known as *S. macromanus* it was logical to consider the modification to be of specific worth; if this specimen were similar to *S. macromanus*, that species would have been considered as more valid. However, with specimens related to two different species showing a parallel mutation, I believe that the condition could best be interpreted as a growth anomaly that may occur in several species of this genus. The fact that this spec-

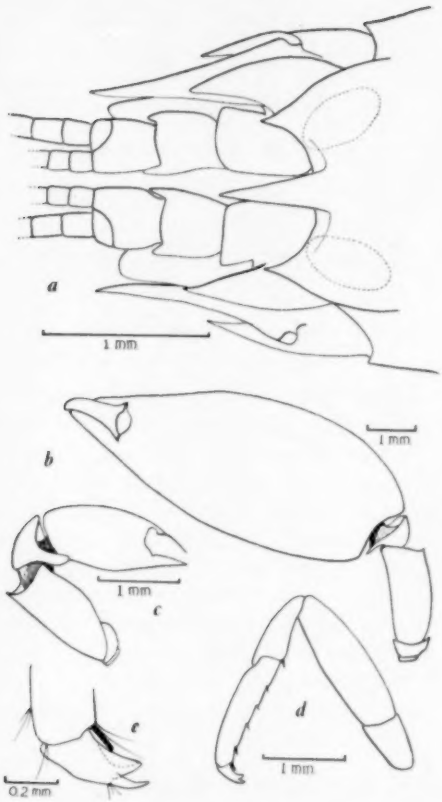

FIG. 3. *Synalpheus charon charon* Banner, aberrant form. *a*, Anterior body region; *b*, inflated large chela and cheliped; *c*, small cheliped of normal form; *d*, third leg; *e*, third leg, dactylus.

imen was one of a sole pair, male and female, the other being plainly *S. charon charon*, collected at one locality would offer support to this conclusion.

If this be so, then the original *S. macromanus* must be considered to be an aberrant form of *S. paraneomeris* Coutière.

Synalpheus paraneomeris Coutière

For synonymy, see Banner, 1956.

LOCALITIES: One specimen at E–1–106, 3 at E–1–306.

Coutierei Group

Synalpheus coutierei Banner

Fig. 4

Synalpheus coutierei Banner, Pacific Sci. 7(1): 36, 1953.

Synalpheus biunguiculatus Coutière, Soc. Ent. de France, Bul. 1898(11): 232, figs. 1–4, 1898 [and other authors—see Banner *op. cit.*].

nec Alpheus biunguiculatus Stimpson, Acad. Nat. Sci. Phila., Proc. 1860: 31.

LOCALITY: Three specimens at E–2–382.

DISCUSSION: These specimens are plainly of this species as illustrated by Coutière (*loc. cit.* and 1905: 873, pl. 31, fig. 8). However, they show slight differences in the proportions of the various parts of taxonomic significance, most apparently in the antennular peduncle, wherein the second article is relatively longer, in the small cheliped, in the dactylus of the third leg, and in the telson. These variations are shown in Figure 4.

Coutière (1898) has shown some variations in the anterior regions and in the dactyli of specimens collected in various parts of the Indian Ocean which approach the differences noted here; he also (1905: figs. 8, 10) described and depicted the form found in the Maldive and Laccadives, and described as a separate variety a form whose variations markedly exceed those of this group of specimens. I believe that considering the variations already reported and the variations in related species of *Synalpheus*, no taxonomic importance should be attached to the slight differences found in these specimens from Arno.

Synalpheus lophodactylus Coutière

Synalpheus lophodactylus Coutière, Soc. Philomath. Paris, Bul. IX, 11(5): 7, 1908.

Synalpheus lophodactylus Coutière, Linn. Soc. London, Trans., Zool. II 17(4): 421, pl. 61, fig. 11, 1921. [Text the same as 1908 reference, plates not previously published.]

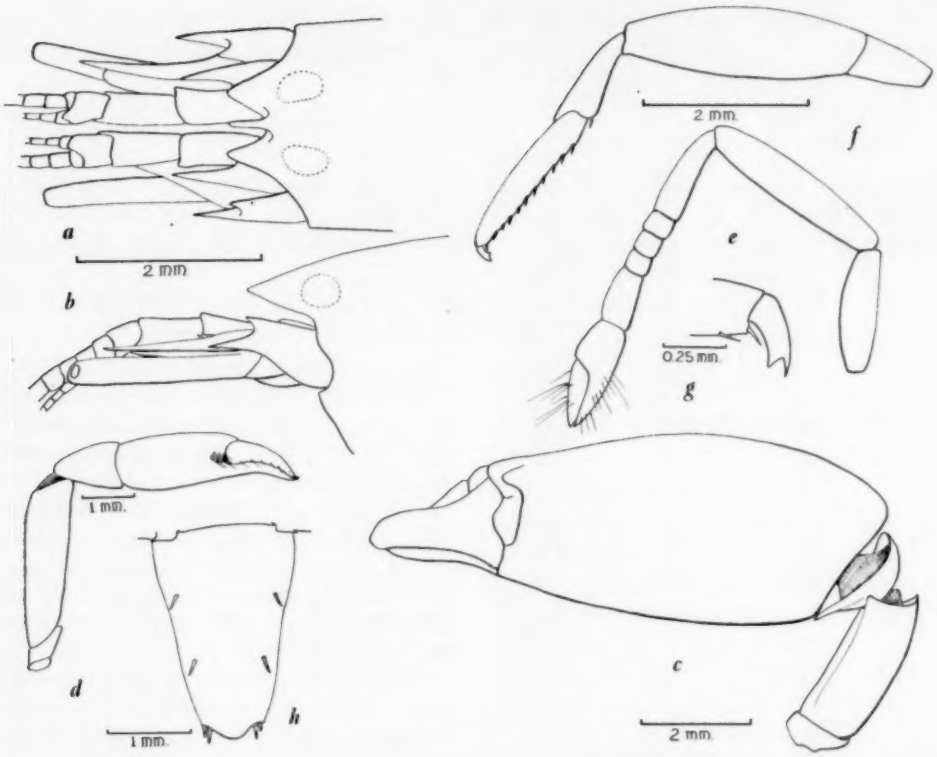

FIG. 4. *Synalpheus coutierei* Banner. *a*, *b*, Anterior body region; *c*, large cheliped; *d*, small cheliped; *e*, second leg; *f*, third leg; *g*, third leg, dactylus; *h*, telson.

LOCALITY: One female, collected at station E–2–343.

DISCUSSION: This specimen agrees well with Coutière's description and figures of his type, the sole specimen reported until now, except for several minor details. The setae on the small chela, shown as a definite tuft and described as "une brosse de soies sériées . . . moins sériées et moins abondantes que dans le groupe *laevimanus* . . .", appear to be less abundant in the distal tuft in this specimen and are also found proximal to the tuft in a row leading towards the articulation. The inferior distal margin of the merus of the third leg bear a feeble movable spine, instead of being unarmed as depicted by Coutière. Finally, the posterior lateral angles of the telson are produced into slender acute teeth almost as long as the lateral distal spines instead of being broader and relatively shorter as shown by Coutière. However, the proportions of the small chela and third legs are almost exactly the same as in the type.

The specimen described by Coutière lacked the large chela, which is intact but slightly distorted in this specimen. It is of typical form for the genus, with the fingers occupying the distal 0.3 of the chela, and the height being about 0.4 of the total length (this proportion may not be accurate because of the condition of the appendage). The merus is 0.5 as long as the chela and 2.5 times as long as broad. The merus and the dactylar articulation are unarmed.

ALPHEUS Fabricius

Megacheles Group

Alpheus deuteropus Hilgendorf, 1878

For synonymy, see Banner, 1956.

LOCALITY: One specimen at E–1–387.

Alpheus collumianus probabalis Banner, 1956

For synonymy of these subspecies and the parent species, see Banner, 1956.

LOCALITY: One specimen from the coral reef at Ine, collected by Wells.

DISCUSSION: The single specimen of this subspecies is markedly more hairy than were the specimens from Saipan; the long setae are especially noticeable on the antennular peduncle, the chelae, and the third and following legs. Moreover, the meri of the third and fourth legs bear 5–6 spines, instead of 4 as in the type, while the merus of the large chela has only 2 small weak spines instead of 6 strong spines that were carried by the type.

Alpheus collumianus medius Banner, 1956

LOCALITIES: Two specimens at E–1–387, 1 at E–1–617.

Macrochirus Group

Alpheus gracilis var. **simplex** Banner, 1953

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–306, both defective; 1 at E–1–387.

DISCUSSION: This single intact specimen is almost identical to the specimens from Hawaii except that it bears a trace of a rostral carina, a condition also noted in one of the aberrant specimens from Hawaii. The external spine of the uropod is black.

The two other specimens are assigned to this species with question for they are lacking their chelae and some of the other appendages. The parts remaining, as well as the structure of the anterior carapace, agree very well with the specimens from Hawaii.

Alpheus ventrosus Milne-Edwards, 1837

For earlier synonymy, see Banner, 1956.

Alpheus sp. Coutière, in Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 882, pl. 74, fig. 19, 1905.

Crangon latipes Banner, Pacific Sci. 7(1): 82, fig. 27, 1953.

LOCALITIES: Four specimens at E–1–290; 3 at E–1–306; 2 at E–1–387; 3 at E–1–617; 5 at E–1–630; 1 at E–2–343.

DISCUSSION: Specimens from station E–1–630 and E–1–290 present an incomplete intergradation from the form described as *C. latipes* and the mature *A. ventrosus*. The intergradation indicated by these specimens is confirmed by specimens from other areas and will be discussed more fully in a subsequent paper. One specimen in this collection shows the darkened spine on the uropods (as discussed in the specimens from Saipan).

Alpheus amirantei Coutière

Alpheus amirantei Coutière, Soc. Philomath. Paris, Bul. IX, 11(5): 15, 1908.

Alpheus amirantei Coutière, Linn. Soc. London, Trans., Zool. II, 17(4): 421, pl. 63, fig. 16, 1921. [Text the same as 1908 reference.]

LOCALITY: One specimen at E–1–611.

DISCUSSION: This specimen appears to be somewhat intermediate in many characters between the type that Coutière described for the Indian Ocean and the Hawaiian form. The relative lengths of the antennular peduncle, antennal peduncle and scaphocerite are subequal, like Coutière's specimen, instead of having the scaphocerite markedly the longest. The basicerite bears a relatively strong spine, like the Hawaiian specimen. This specimen, a female, has slightly longer fingers to the large chela than does the Hawaiian form. The second carpal article of the second leg is 2.7

times the length of the first, instead of 2.3 in the Hawaiian form, and 3.0 in Coutière's. The inferior distal tooth of the merus of the third leg is longer and more acute than in the Hawaiian form, therefore more like the type specimen. Finally, the Arno specimen is unlike both previous forms in the armature of the merus of the large and small chela. In Coutière's specimen the inferior internal margin of the merus carried a series of rounded serrations terminating in a strong acute tooth; in the Hawaiian specimens the serrations were lacking, and the tooth was weaker; in the Arno specimen the tooth also is lacking. The merus of the small chela was armed with a tooth in the type but in both the Hawaiian and Arno specimens the tooth is lacking.

However, as the specimen agrees well with the general description of *A. amirantei*, these differences are considered to be at most subspecific, and are more likely to be individual variation.

Alpheus nanus (Banner) 1953

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–306.

DISCUSSION: Like the specimens from Saipan, the sole specimen with the chelae intact, a male, had spinules on the inferior internal margin of the merus; both large and small chelae had seven such spinules. The other specimen, a female, was lacking in both chelae.

Alpheus paragracilis Coutière, 1897

For synonymy, see Banner, 1956.

LOCALITIES: One specimen at E–1–106; 2 at E–1–285; 3 at E–1–387; 2 at E–1–617.

Alpheus macrochirus Richters

Alpheus macrochirus Richters, Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164, pl. 17, figs. 31–33, 1880.

nec Alpheus macrochirus de Man, Arch. f. Naturgesch. 53(1): 519, 1887.

LOCALITIES: Two specimens at E–1–306; 2 at E–2–360.

DISCUSSION: These specimens agree well with the short original description, with the characteristics given in de Man's key and discussion (1911) and with the three figures in Coutière's *Les Alpheidae* (1899, figs. 51, 52, 261).

Crinitus Group

Obesomanus Subgroup

Alpheus lutini Coutière, 1905

For synonymy, see Banner, 1956.

LOCALITIES: Three specimens at E–1–106; 12 at E–1–122; 30 at E–1–149; 5 at E–1–285; 5 at E–1–290; 16 at E–1–306; 5 at E–1–387; 5 at E–1–611; 1 at E–2–343; 1 at E–2–382.

DISCUSSION: One specimen preserved in formaldehyde has a body colored pale lemon yellow, intensifying to bright lemon yellow on the legs. The anterior region of the carapace and the antennular and antennal bases are orange-red; the small and especially the large chelae are lemon yellow at the proximal ends, changing to almost blood red at the tips. Some other specimens show a similar color pattern except that the red of the tips of the chelae is restricted to irregular patches surrounded by white. It is not known how well this pigmentation parallels that found in the living specimens.

Crinitus Subgroup

Alpheus alcyone de Man

Alpheus alcyone de Man, Senckenb. Naturf. Gesell. Abhandl. 25: 870, pl. 27, fig. 61, 1902.

Alpheus aculeipes Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 892, pl. 79, fig. 31, 1905.

Alpheus alcyone de Man, Siboga Exped. 39a[1] (2): 351.

LOCALITIES: One specimen at E–1–285; 1 at E–1–611; 1 at E–1–617; 1 at E–1–648; 5 at E–2–382.

Alpheus arnoa sp. nov.

Fig. 5

TYPE SPECIMEN: A non-ovigerous female, 12.2 mm. long, collected on Arno Atoll, Marshall Islands, by R. W. Hiatt at station E–2–343. Only specimen known.

DESCRIPTION: Frontal region of carapace extending considerably beyond eyes. Rostrum short, triangular, reaching about 0.5 the length of visible portion of first antennular article; dorsally bearing a strong and abrupt carina that extends to slightly posterior of gastric region. Orbital hoods rounded, somewhat inflated, anteromedially extending into flattened area, at highest about equal in height to dorsal carina, laterally demarked by an abrupt groove from carapace which covers base of antennal peduncle. Orbitocarinal groove shallow and rounded; orbitorostral area flattened.

Second antennular article slightly less than twice as long as broad, 1.5 times as long as visible portion of first article, 1.7 times as long as third article; diameter only 0.6 that of the first article. Stylocerite acute, with tip reaching almost to end of first article. Basicerite unarmed. Scaphocerite with lateral margin strongly concave, spine heavy, somewhat blunt, reaching beyond end of antennular peduncle; squamous portion narrow and shorter, reaching to middle of third antennular article. Carpocerite reaching to end of scaphocerite.

Large chela subcylindrical, slightly tapering, entire, 2.8 times as long as broad, with the fingers occupying the distal 0.3. Dactylus arched and rounded, calcified and white distally. Tip of fixed finger similarly calcified. Merus 0.37 as long as chela, with outer face 1.8 times as long as broad; all margins unarmed, but inferior internal margin projecting into a low but strong extension. Chela with only sparse scattered setae. Small chela 3.5 times as long as broad, with simple conical fingers occupying the distal 0.38. Carpus somewhat elongate. Merus slightly longer (about 10%) than that of large cheliped, 2.5 times as long as broad, also unarmed. Chela bearing a moderate growth of setae on superior distal face.

Carpus of second legs with the ratio: 10: 21:8:7:11.

Ischium of third legs bearing strong tooth. Merus 4 times as long as broad, armed with a strong acute tooth distally. Carpus unarmed except for poorly developed distal inferior tooth, 0.3 as long as merus. Propodus 3.5 times as long as broad, 0.66 as long as merus, armed on inferior margin with five strong spines and five weaker spines. Propodus and dactylus with usual scattered sparse setae. Dactylus curved, simple, and well developed. Fourth legs of similar armature and proportions.

Telson 2.4 times as long as posterior margin is broad, anteriorly 1.4 times as broad as posteriorly, sides with slight taper; anterior pair of dorsal spines 0.39, posterior pair 0.60 of length posterior from articulation; distal lateral spines moderately strong; strongly arcuate distal margins armed with numerous short heavy spines. Outer uropod with strong lateral spine and with distal margin armed with numerous shorter spines in addition to usual setae. Inner uropod bearing eight strong spines on distolateral margin and numerous short heavy spines similar to those of the telson along distal margin.

DISCUSSION: This species belongs to the Crinitus subgroup, and within the subgroup it appears to be most closely related to those other species with an extended dorsal carina, *A. bucephaloides* Nobili, *A. longecarinatus* Hilgendorf, and *A. parvus* de Man. From the first two species it can most easily be distinguished by the lack of spines on the carpus of the third legs. *A. parvus* lacks the armature of the carpus, like this species, but the configuration of the anterior margin of the cara-

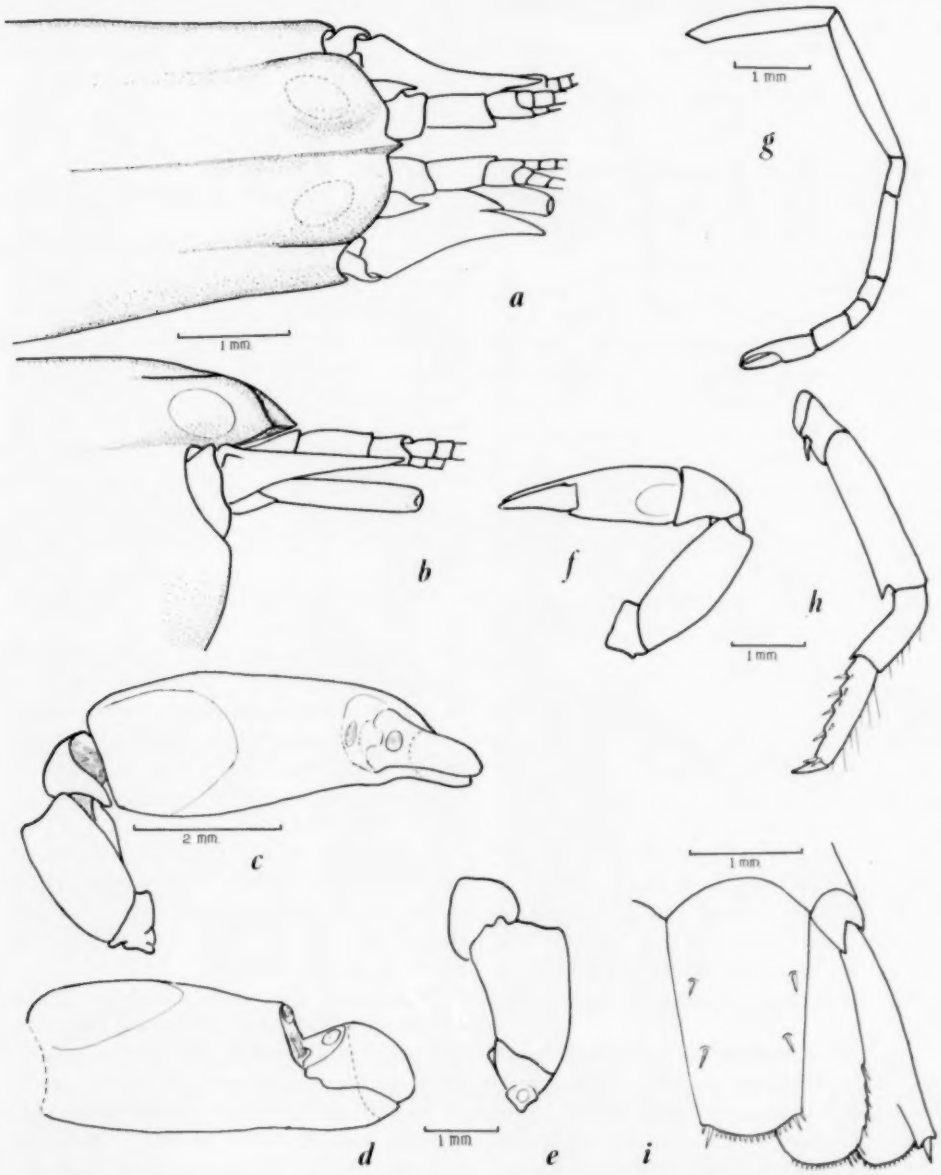

FIG. 5. *Alpheus arnoa* sp. nov. *a*, *b*, Anterior body region; *c*, large cheliped, lateral aspect; *d*, large chela, inferior aspect; *e*, large cheliped, merus, medial aspect; *f*, small cheliped; *g*, second leg; *h*, third leg; *i*, telson and uropods.

pace is different, (compare Fig. 5*a* to de Man, 1911, pl. 15, fig. 74), the flattened portion of the scaphocerite is longer and more narrow, the second carpal article is only 1.3 instead of 2.1 times as long as the first, the telson is more tapering and the spines and spinules of the uropods and telson were unreported by de Man.

The specific name refers to the type locality.

Alpheus bucephalus Coutière

Alpheus bucephalus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 890, pl. 78, fig. 29, 1905.

Alpheus consobrinus de Man, Leyden Rijks Mus. van Naturlijke Hist. Zool. Meded., Notes 30:101, 1908.

Alpheus consobrinus de Man, Siboga Exped. 39a[1]: 360, pl. 16, fig. 75, 1911.

LOCALITIES: One specimen at E–1–122; 11 at E–1–306; 4 at E–2–360.

DISCUSSION: *A. consobrinus* was recognized by de Man as being closely related to *A. bucephalus* and *A. clypeatus* Coutière, but was separated by him on the basis of the following characteristics:

1. The scaphocerite is slightly longer than the carpocerite in *A. consobrinus* and slightly shorter in *A. bucephalus*.

2. The basicerite is armed with a minute tooth in *A. consobrinus* and unarmed in *A. bucephalus*.

3. The merus of the large chela bears an acute tooth on the inferior internal margin in *A. consobrinus* while in *A. bucephalus* the corresponding projection is rounded.

4. The small chela is usually dimorphic in *A. consobrinus*, the males bearing an expanded dactylus with a fringe of setae, while in *A. bucephalus* the dactylus of the small chela of the male is narrow, conical and without a fringe of setae, a condition similar to that of the females.

5. The second article of the second leg is three times the length of the first in the males of *A. consobrinus* while in both sexes of *A. bucephalus* (according to de Man's key) it is "more than twice as long as the first." (However, Coutière's figure 29c shows it to be about 2.75 times as long as the first.)

6. The telson is slightly more narrow in *A. consobrinus*, the length-breadth ratio being 2.6, while in *A. bucephalus* where the ratio is 2.2.

This impressive list of differences would lead one to believe that the species are separate and distinct. However as previously reported from Saipan, the broadening of the dactylus of the males is not a constant characteristic. In this series of specimens a group collected at E–1–306 shows that each one of these characteristics is individually variable. In Table 1 a tabulation of these characteristics of 10 intact specimens is given. The relative lengths of the scaphocerite and carpocerite are quite variable; the spine of the basicerite is present in only two specimens; the meral spine of the large chela varies from strong and acute to low and rounded; the dimorphic character of the small chela of the males does not seem to be correlated with size or other characteristics; the ratio of the first two secondary articles of the second leg varies from 1.7, a figure below that of *A. bucephalus*, to 3.5, a figure above that of *A. consobrinus;* and, finally, the telsal length-breadth ratio ranges from 2.1 to 2.9, the last in the smallest specimen. Moreover, the variations are not correlated with each other, so a specimen like *A. consobrinus* in the sexually dimorphic chela does not have the tooth on the basicerite, etc.

These variations parallel or exceed the variations previously reported upon for the closely related *A. clypeatus* Coutière and *A. brevipes* Stimpson (Banner, 1953: 103–110). I believe that when sufficient specimens are examined from all parts of the range of these four nominal species, it is very likely that the species will all be found to be part of a single, very variable species. However, the present series of specimens do not offer enough direct evidence to warrant this lumping except to combine *A. consobrinus* with *A. bucephalus*.

TABLE 1
VARIATION IN ONE SAMPLE OF *Alpheus bucephalus* COUTIÈRE

Sex	Length, mm.	Length of scaphocerite compared to carpocerite	Tooth on basicerite	Tooth on merus of large cheliped	Length of second carpal article ÷ length of first	Telson, length ÷ breadth at base	SMALL CHELA OF MALES								
							Length Palm, mm.	Length Dactyl, mm.	Length Palm ÷ length, Dactylus	Breadth Dactylus at base, mm.	Length Dactylus ÷ breadth	Breadth Dactylus 0.3 distance from base, mm.	Ratio, breadths of Dactylus	Setae	Sexual Dimorphism
♀ *	13.4	equal	abs	strong, acute	1.7	2.2									
♀ *	11.2	scaphocerite longer	pres	strong, acute	2.3	bro-ken									
♀ *	10.3	equal	abs	low, obtuse	2.7	2.3									
♀	6.5	equal	abs	lacking	1.8	2.8	A	B	A/B	C	B/C	D	C/D	..	..
♂	9.3	scaphocerite longer	abs	low, rounded	1.9	2.1		(lacking)					(lacking)		
♂	8.7	carpocerite longer	abs	strong, obtuse	2.5	2.4	1.07	1.04	1.0	0.40	2.7	0.40	1.0	fringe	yes
♂	8.5	carpocerite longer	abs	strong, acute	3.5	2.6	1.15	0.95	1.3	0.29	3.3	0.22	1.4	scattered	no
♂	8.1	scaphocerite longer	abs	strong, acute	2.8	2.5	1.00	1.00	1.0	0.37	2.9	0.37	1.0	fringe	yes
♂	8.1	carpocerite longer	pres	strong, acute	2.9	2.1	1.18	1.33	0.9	0.51	2.6	0.55	0.9	fringe	yes
♂	7.6	carpocerite longer	abs	low, rounded	2.2	2.9	1.00	0.62	1.7	0.29	2.1	0.15	1.9	scattered	no

* Ovigerous females

Alpheus clypeatus Coutière

Alpheus clypeatus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 897, pls. 81–82, fig. 36, 1905.

LOCALITIES: Three specimens at E–1–306 (fragmentary and uncertain); 4 at E–1–617; 5 at E–1–648; 4 at E–2–343.

Alpheus pachychirus Stimpson, 1860

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–290.

Alpheus frontalis H. Milne-Edwards, 1837

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–611.

Diadema Subgroup

Alpheus bidens (Olivier)

Palaemon bidens Olivier, Encyclopédie Méthodique, Histoire Naturelle 8: 663, 1811.
Alpheus bidens H. Milne-Edwards, Histoire Naturelle des Crustacés 2: 353, pl. 24, figs. 11, 12, 1837.
Alpheus tridentatus Zehntner, Rev. Suisse de Zool. 2: 204, pl. 8, fig. 24, 1894.

LOCALITIES: Two specimens at E–2–360; 1 at E–2–382.

DISCUSSION: These specimens show considerable variation from each other despite the fact that there are only three specimens involved. On one specimen the dorsal denticles of the anterior carapace reach almost to the base of the eyes, while the other two are considerably shorter (but not placed as far posteriorly as indicated by de Man, 1911: pl. 17, fig. 80). The rostrum on one does not reach quite to the end of the first antennular article, on the second reaches slightly beyond it, and on the third reaches almost to the middle of the second article. The first antennular article bears one movable spine and two long setae in two of the specimens, but in the third carries one spine on one side and two spines (as shown by de Man) on the opposite article. On the merus of the large chela the armature varies, with one specimen bearing feeble spines on the inferior internal margin, only several exceedingly weak spines on superior margin, while the inferior external margin carried only about 10 poorly developed serrations; on the second specimens the spines of the inferior internal are quite strong, the superior margin carries 7 short but strong spines, and the serrations on inferior external margin are marked; the third specimen is intermediate between these two.

However in other characteristics, these specimens compare sufficiently well to the descriptions of the species that these variations cannot permit one to consider them as other than this species.

Alpheus diadema Dana, 1852

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–149; 1 at E–1–290; 2 at E–2–343; 2 at E–2–360.

Alpheus percyi Coutière

Alpheus percyi Coutière, Soc. Philomath. Paris, Bul. 9(5): 21, 1908.
Alpheus percyi Coutière, Linn. Soc. London, Trans., Zool. II, 17(4): 426, pl. 64, fig. 22, 1921. [Same description, figures added.]

LOCALITY: Two specimens at E–2–382.

DISCUSSION: This specimen agrees very well with the specimens from the Hawaiian archipelago except for the rostrum. In the Hawaiian species the rostrum bears a low, obtuse but definite crest, but in these two specimens the rostrum is dorsally flat and smooth. While Coutière does not discuss this characteristic in his original description, his figures in his 1921 publication (figs. 22, 22[1]) seem to indicate a condition similar to these Marshall specimens. It may be that the Hawaiian specimens will be found to represent a geograph-

ically isolated subspecies, but not enough specimens are known to draw any conclusions as yet.

Alpheus gracilipes Stimpson, 1860

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–306; 2 at E–1–387; 3 at E–1–617.

DISCUSSION: Of these 7 specimens, 2 males and 2 females had their small chelae intact; all 4 had the characteristic fringe of hair over the dactylus, but none had their fingers noticeably broadened. These specimens, therefore, are like the form found in Hawaii and not like the form from the Marianas.

Alpheus paracrinitus var. **bengalensis** Coutière, 1905

For synonymy, see Banner, 1956.

LOCALITY: One specimen at E–1–106.

Edwardsi Group

Alpheus crassimanus Heller

Alpheus crassimanus Heller, Reise der . . . Novara . . . Zool. Theil 2(8): 107, pl. 10, fig. 2, 1865.

LOCALITIES: One specimen at E–1–387; 2 (fragmentary) at E–1–670; 3 at E–2–311.

DISCUSSION: The fragmentary specimens were assigned to this species because those parts remaining were almost identical to specimens of similar size from Hawaii.

One specimen was somewhat unlike the rest with the sculpturing on the large chela deeper and more abrupt, and the second and third legs thinner and more elongate (the merus of the third legs is 6 times as long as broad instead of the reported 4.5 to 5.0 times). However similar variation in the large chela has been reported for Hawaiian specimens (Banner, 1953: 134), and for this comparison, the meri of a group of specimens collected from a single area in Kaneohe Bay, Oahu, Hawaii, were measured, and it was found that the length-breadth ratio varied from 4.5 to 6.0.

Alpheus strenuus Dana

Alpheus strenuus Dana, U. S. Explor. Exped. 13(1): 543, pl. 34, fig. 4, 1852.

LOCALITIES: One specimen at E–2–169; 6 specimens, Arno, records lost.

DISCUSSION: Some of these specimens, the largest I have yet seen, reach a total body length of 57 mm.; Coutière (1905: 913) has reported specimens reaching 95 mm., but his figures included the chelae.

The distinction between this species and *A. audouini* described by Coutière in 1905 appears to be somewhat questionable. Coutière makes the distinction upon the form of the anterior carapace and rostrum, and the form of the large chela, but the distinctions are so fine as to be scarcely apparent in his figures. Considering the variations that have been reported for other species of the genus, these fine distinctions appear to be of dubious validity. Probably the best differentiations may be found in the antennular base, where the median article is 1.5 times the length of the distal article in *A. audouini* and 2 times the length in *A. strenuus;* in the second legs, where the first article is 1.65 times the length of the second in *A. audouini* and 1.0 to 1.2 times the length in *A. strenuus;* and in the merus of the third legs where the length is 4.3 times the breadth in *A. audouini* and 3.7 times the breadth in *A. strenuus*. Even these differences could easily be within the normal range of variation for an inherently variable species.

Alpheus pacificus Dana, 1852

For synonymy, see Banner, 1956.

LOCALITY: Three specimens at E–1–106.

Alpheus dolerus Banner

Alpheus dolerus Banner, Pacific Sci. 10 (3): 362, fig. 2.

LOCALITIES: One specimen each at E–1–617 and E–2–343.

DISCUSSION: While these specimens compare well to the types and paratypes from Saipan, positive identification is impossible because both are females, and males are necessary for identification in this group.

Alpheus parvirostris Dana, 1852

For synonymy, see Banner, 1956.

LOCALITIES: Three specimens at E–1–106; 11 at E–1–122; 9 at E–1–149; 1 at E–1–285; 1 at E–1–290; 6 at E–1–306; 1 at E–1–387; 1 at E–1–611.

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Systematic Anatomy of *Hesperomannia*

SHERWIN CARLQUIST[1]

THE GENUS *Hesperomannia* (Compositae, tribe Mutisieae) has attracted interest because of its arborescent habit, its restriction to certain of the Hawaiian Islands, and its rarity in the locations in which it is found. The purpose of the present paper is to survey the anatomical diversity which exists in the genus and relate it to gross morphological characters in an attempt to achieve an acceptable classification. The affinities of *Hesperomannia*, as suggested particularly in terms of anatomical characters, are to be discussed in later studies. Within the genus, however, anatomical features seem illuminating in demonstrating the most natural taxonomic groupings.

ACKNOWLEDGMENTS

The writer wishes to express appreciation to the curators of the herbaria named below for loan of specimens. Dr. Harold St. John of the University of Hawaii kindly conducted a field trip on which the writer was able to collect material of *Hesperomannia*. Acknowledgment is offered to Dr. Reed C. Rollins and Dr. Grady Webster for reading the manuscript and suggesting improvements.

MATERIALS AND METHODS

Vegetative material of the writer's collection of *H. arborescens* subsp. *Swezeyi* was fixed in a Carnoy's solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). All other material was prepared from herbarium specimens as follows. Vegetative and floral parts were treated with warm 2.5 per cent aqueous NaOH to remove cell contents and expand structures to their original condition. Further clearing was achieved by treatment with a 250 per cent chloral hydrate solution. After washing, whole mount preparations of flowers and leaves were made by dehydration in an ethyl alcohol series, staining in a 1 per cent safranin solution in absolute ethyl alcohol, transferring to xylene, and mounting in xylene-soluble synthetic resin. Portions of both the Carnoy's-fixed material and the "revived" herbarium material were prepared for sectioning according to the tertiary butyl alcohol schedule of Johansen (1940: 130–131). Treatment with hydrofluoric acid prior to infiltration was necessary for softening woody structures. Sections were stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940: 92–93). All of the collections for which anatomical data were assembled are represented in the Bernice P. Bishop Museum in Honolulu, except where otherwise noted. Duplicates of many of these specimens are in other herbaria.

ANATOMY

The Leaf

Examination of young leaves near the shoot apex of *Hesperomannia arborescens* subsp. *Swezeyi* showed them to be densely covered with uniseriate nonglandular hairs (Fig. 1). Interspersed among these are biseriate glandular trichomes. At such an early stage, virtually every epidermal cell on both surfaces

[1] Rancho Santa Ana Botanic Garden, Claremont, California. Manuscript received February 9, 1956.

FIG. 1. Longitudinal section of young petiole of *Hesperomannia arborescens* subsp. *Swezeyi* (*Carlquist H3*), × 170. Short biseriate glandular hairs may be seen near the epidermis (below), interspersed among crowded uniseriate nonglandular hairs, which cover most of the photograph.

of the leaf bears a trichome of one of these types. This condition is true of all of the species. A preparation of the most glabrous species, *H. Lydgatei*, showed an identical situation. During enlargement of the young leaf of *H. arborescens* subsp. *Swezeyi*, there is a tendency for the uniseriate trichomes to degenerate and slough off. In Figure 1, the uniseriate trichomes already show an accumulation of dark-staining resinous contents, indicating the beginning of their decline relatively soon after formation. Upon maturation of the leaf of this plant (Fig. 2), uniseriate hairs have disappeared altogether, except for occasional persistent basal cells. Simultaneously, the biseriate glandular trichomes increase in size and become sunken into pockets as the mesophyll expands.

Differences in leaf indument, which are treated here as important characters of the species, may be explained on the basis of differential elimination of trichomes during maturation of the leaf. In *H. arbuscula* subsp. *oahuensis*, for example, uniseriate hairs are retained, particularly on the young stems and lower surfaces of leaves (Fig. 3). In this species, uniseriate hairs, particularly the terminal cell of each, become sclerified, corresponding with their persistence. Biseriate glandular hairs are also present on the mature leaf of *H. arbuscula* subsp. *oahuensis*. Although less numerous, both types of trichomes may also be found on mature leaves of *H. arbuscula* subsp. *arbuscula*. *Hesperomannia arbuscula* is the only species in which uniseriate trichomes are retained on the mature leaf.

In *H. Lydgatei*, *H. arborescens* subsp. *arborescens*, subsp. *Bushiana*, and some populations of subsp. *Swezeyi* (*Judd 1244*, for example), both types of trichomes disappear early in leaf ontogeny. In leaves of these taxa, a heavy cuticle is formed on both adaxial and abaxial epidermis.

Variations in leaf thickness occur in all the species, and cannot be considered as a constant taxonomic character.

Peduncle

Among the taxa recognized here under *H. arbuscula* and *H. arborescens*, little variation in

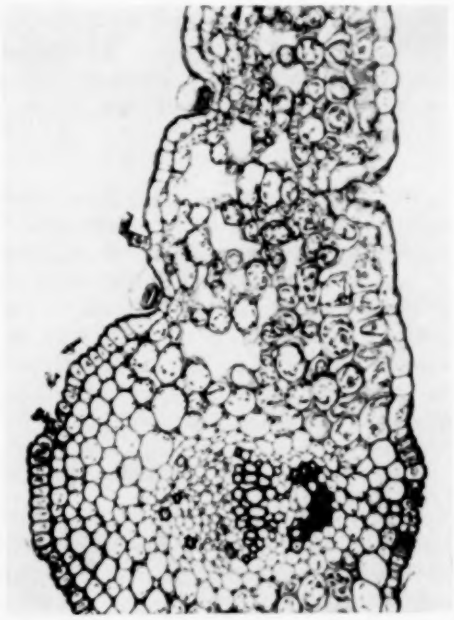


FIG. 2. Transection of a mature leaf of *Hesperomannia arborescens* subsp. *Swezeyi* (*Carlquist H3*), × 130. Abaxial epidermis at left. Note vein, accompanied by sclerenchyma, remnants of uniseriate hairs on the abaxial surface, and sunken glandular hairs.

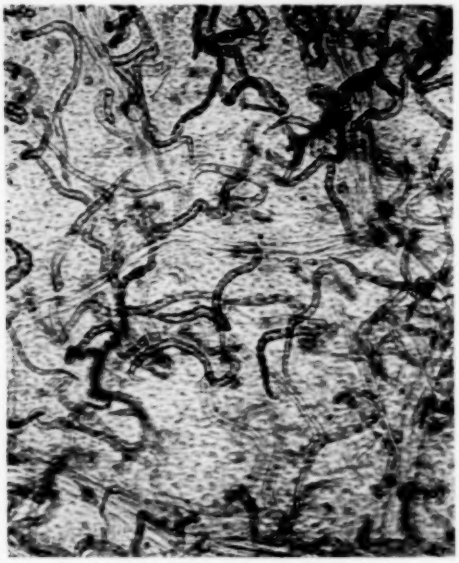


FIG. 3. Lower surface of mature leaf of *Hesperomannia arbuscula* subsp. *oahuensis* (*Hillebrand 1871*), × 140. Numerous sclerified hairs may be seen above the vein reticulum.

peduncle size or structure occurs. A peduncle of *H. arborescens* subsp. *Bushiana*, shown in Figure 4A, is typical in its numerous bundles and sclereid nests. Trichomes are persistent on the epidermis of peduncles in these two species. *Hesperomannia Lydgatei*, on the contrary, shows peduncles much smaller in diameter. This smaller stature is reflected anatomically in the fewer bundles present in the vascular cylinder and in the much smaller size of the pith (Fig. 4B). In addition, no hairs are present on the peduncle epidermis of *H. Lydgatei*, which is covered by a prominent cuticle.

Involucral Bracts

As in peduncle anatomy, the involucral bracts of plants belonging to *H. arbuscula* and *H. arborescens* are comparatively uniform in anatomical structure. As shown for *H. arborescens* subsp. *Suezeyi* in Figure 4C, a thick region of subhypodermal fibers occurs near the outer face of the bract in these species. Epidermal and hypodermal cells on this surface remain thin-walled. This zone of fibers may be as many as 14 cells in thickness. On the interior face of the bract, a thinner band of fibers is present. The adaxial epidermis is most heavily sclerified, with decreasing wall thickness on the two or three cell layers interior to it. Between the fibers on the inner and outer faces of the bract, a region of thin-walled parenchyma is present. A single series of vascular bundles occurs in this region. The thickness of this central parenchyma band is greatest near the base of the bract and decreases toward the apex.

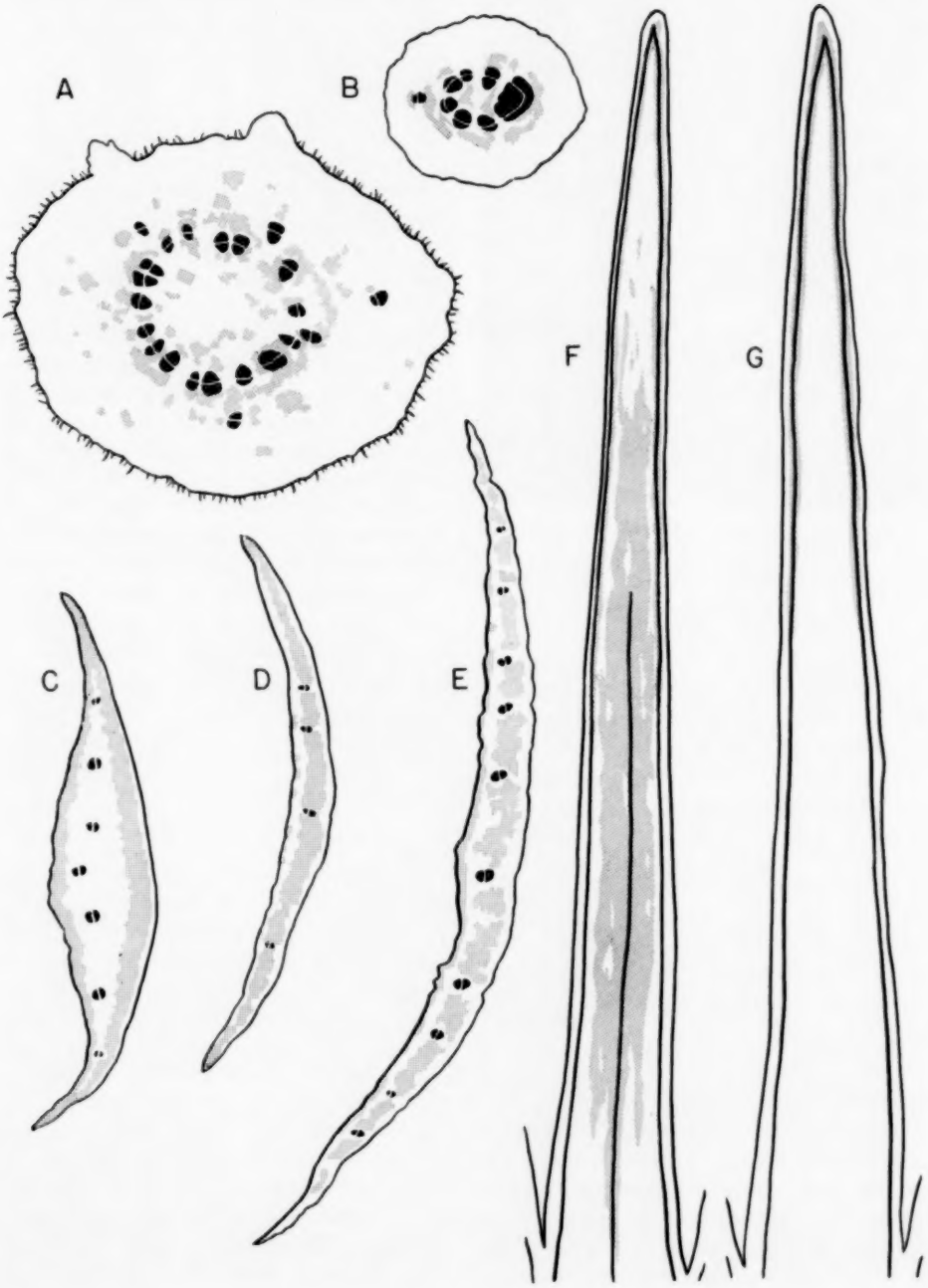
Inner involucral bracts show an altered form of this structure in the two species, as the bract of *H. arborescens* subsp. *Bushiana* in Figure 4D demonstrates. In such a bract, the region of parenchyma between the two bands of fibers is greatly narrowed. The bundles occur at points within the outer band of fibers, rather than in the parenchyma. The outer band of fibers is continuous, or nearly so, and encases most of the bundles.

The involucral bracts of *H. Lydgatei* show a structure comparable only to the inner involucral bracts of the other species. Bundles occur only in interstices between the strands of fibers, which never form a continuous band as they do in the bract of *H. arborescens* subsp. *Bushiana* described above.

Corolla

As is typical for Compositae, a pair of lateral veins, which fuse beneath each sinus, is present in each corolla lobe in *Hesperomannia* flowers. In addition, median veins, such as shown in Figure 4F, were found to be present in both subspecies of *H. arbuscula* as well as in *H. arborescens* subsp. *Suezeyi*. Such median veins are present in one to three of the larger corolla lobes of a flower in these taxa, or are absent in some flowers. Where present, they extend for varied distances in the lower portion of the lobe. No median veins were found in the taxa not mentioned.

Fibers encase the upper extent of the lateral veins of corolla lobes (Fig. 4F, G) in all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species. In addition, subepidermal cells interior to the lateral veins of the lobe may become sclerified; such diffuse sclereids were found in all the subspecies of *H. arborescens* and *H. arbuscula*. The extent of these sclereids is shown diagrammatically in Figure 4F for *H. arborescens* subsp. *Swezeyi*, in which they were abundant. They were least abundant in *H. arbuscula* subsp. *arbuscula*, and altogether lacking in *H. Lydgatei* (Fig. 4G). Sclereids of this type appear in the young flowers, and increase in size until the corolla withers. As shown in Figure 5, these sclereids become impacted against each other, forming blunted ends and distorted shapes. Because of the presence of such sclereids, median veins in corolla lobes can be detected with certainty only in cleared preparations. Although sclereids of this nature have never been reported in the Compositae before, they have been found by the writer in a number of Mutisieae.

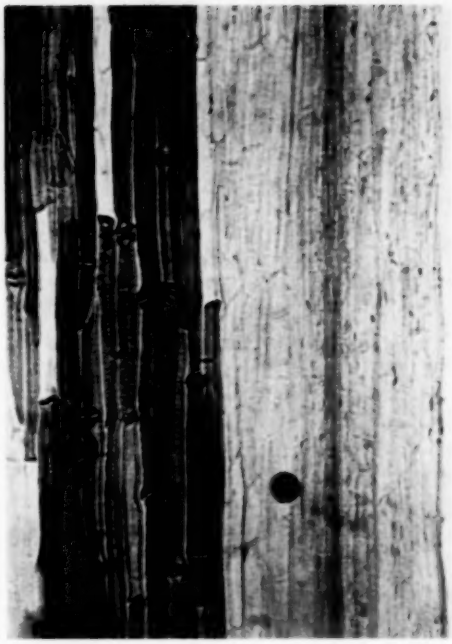

FIG. 5. Portion of cleared corolla-lobe of *Hesperomannia arborescens* subsp. *Swezeyi* (*Judd 1244*), × 175. Margin of lobe at right; inward from the margin may be seen the lateral vein, a glandular hair (out of focus), and a number of subepidermal sclereids, left.

EVOLUTION WITHIN THE GENUS

Characters of gross morphology alone give few suggestions concerning presumed evolutionary advancement within *Hesperomannia*. One feature which deserves mention is the tendency toward aggregation of heads. In most Mutisieae, particularly putatively primitive genera, the heads are solitary and terminal. In *Hesperomannia*, they may be solitary, but are more frequently in clusters of 2 to 10. Where fewer peduncles are present, they are borne coordinately at the end of an axis. Where more numerous peduncles form a cluster, some peduncles may branch from others. If more than one head is present, no leaves or bracts subtend the additional heads. In view of the fact that clusters of heads are present in all of the taxa except *H. arborescens* subsp. *Bushiana*, which would appear to be derived on other grounds, such clusters may have been primitively present in *Hesperomannia*, despite the solitary condition elsewhere in the Mutisieae.

Anatomical characters seem to offer more reliable criteria of primitiveness, though few features can be cited in this regard. The caducous hairs on herbage and peduncles may be interpreted in this connection. One would expect the development of mature trichomes to be more primitive than the condition where they are lost at an early stage. In this case, *H. arbuscula* shows the most primitive expression of this character. *Hesperomannia Lydgatei* shows the most advanced condition,

←FIG. 4. A, B, transections of peduncle near base, × 30. A, *Hesperomannia arborescens* subsp. *Bushiana* (*Degener 11927a*); B, *H. Lydgatei* (*Forbes 190K*). C–E, transections of involucral bracts, midway along length of bract, × 21. C, *H. arborescens* subsp. *Swezeyi* (*Judd 1244*), outer bract; D, *H. arborescens* subsp. *Bushiana* (*Degener 11927a*), inner bract; E, *H. Lydgatei* (*Forbes 190K*), outer bract. F, G, corolla lobes, × 15. F. *H. arborescens* subsp. *Swezeyi* (*Judd 1244*); G, *H. Lydgatei* (*Forbes 190K*). Outlines and veins shown in black, sclerenchyma shaded.

since it lacks trichomes on both mature leaves and peduncles. *Hesperomannia arborescens* shows intermediate stages, since uniseriate hairs are present on peduncles, though lacking on mature leaves. Biseriate glandular trichomes have likewise disappeared from mature leaves in some populations of this species.

The involucral bracts of *H. Lydgatei* may be interpreted as advanced in their structure. Likewise, the lack of median veins in corolla lobes of this species, despite optimal lobe-width, would seem to be an advanced characteristic. Absence of median veins in flowers of *H. arborescens* subsp. *arborescens* and subsp. *Bushiana* may similarly be interpreted as reductions, if the generally-accepted tenet of Koch (1930: 940) that median veins are primitively present in the family is correct.

Thus, *H. arbuscula* would seem to possess the more primitive characteristics. *Hesperomannia arborescens* shows somewhat more advanced features, while *H. Lydgatei* is differentiated from the other species by characters which seem best interpreted as the most advanced condition in the genus.

SYSTEMATIC TREATMENT AND DISCUSSION

The writer has had the privilege of studying type or isotype material of all of the species of *Hesperomannia*. In addition, the collections of the three largest assemblages of specimens of this genus, those of the Bishop Museum, the Gray and Arnold herbaria at Harvard, and the Herbarium of the University of California, Berkeley, have been examined. This comparatively large amount of material has permitted a more comprehensive picture of species variability than has previously been available. The descriptions of Degener (1946) are adequate for indicating some of the extremes of variation, particularly in the complex recognized here as *H. arborescens*. These descriptions do not incorporate the intermediate expressions of characters that are found in many specimens, however, and the discussions following each of the taxa below emend these descriptions where necessary, suggesting the most constant characters for each taxon recognized.

KEY TO SPECIES AND SUBSPECIES

1A. Peduncles 1.8 mm. in diameter or less, glabrous; inner involucral bracts 3.5 to 5 cm. long; corolla lobes without diffuse sclereids . . . . . **H. Lydgatei**

1B. Peduncles 3 mm. in diameter or more, bearing hairs even at maturity; inner involucral bracts 3.3 cm. long or less; corolla lobes with diffuse sclereids in subepidermal layers 2

2A. Leaves elliptic, the lamina base acute; abaxial surface of mature leaf covered with numerous uniseriate sclerified hairs . . . . . 3. **(H. arbuscula)**

3A. Straggling shrub; hairs on abaxial surface of leaf relatively sparse; diffuse sclereids in corolla lobes infrequent; West Maui . . . . . **H. arbuscula** subsp. **arbuscula**

3B. Tree; abaxial surface of leaf densely coated with hairs; numerous diffuse sclereids present in corolla lobes; Waianae Mts., Oahu . . . . . **H. arbuscula** subsp. **oahuensis**

2B. Leaves lanceolate to oblanceolate or obovate, the lamina base acuminate; no uniseriate hairs present on mature leaves . . . . . 4. **(H. arborescens)**

4A. Achenes at maturity 12–14 mm. long; no median corolla veins present; Lanai . . **H. arborescens** subsp. **arborescens**

4B. Achenes at maturity 12 mm. or less in length; median corolla veins present or not; Koolau Mts., Oahu 5

5A. Heads solitary or in clusters of 2 to 10; heads containing 30 or more flowers; median veins present in some corolla lobes . . **H. arborescens** subsp. **Swezeyi**

5B. Heads solitary, containing approximately 25 flowers; no median veins in corolla lobes . **H. arborescens** subsp. **Bushiana**

1. **Hesperomannia Lydgatei** Forbes

Hesperomannia Lydgatei Forbes, Bernice P. Bishop Mus., Occas. Paper 4: 220, 1909.

This species is the most distinct in the genus, by virtue of its geographic isolation (endemic to Kauai) and numerous morphological and anatomical features. As shown above, the peduncles are glabrous and markedly narrower than those of the other species. The long, lanceolate involucral bracts are distinctive both in size and shape and in their anatomy. The lack of diffuse sclereids in corolla lobes has been mentioned earlier. In features of vegetative anatomy, however, no differences can be found between *H. Lydgatei* and the other species. The leaves and stems were found to be identical in shape and anatomy to some plants referred here to *H. arborescens* subsp. *Swezeyi* (*Judd 1244*, for example). Consequently, the difference in these respects suggested by Forbes (1909: 220) cannot be maintained. Although it has not been collected since 1910, this species may still be extant.

Representative specimens—Kauai, Wahiawa Mts.: *Lydgate, May 1908* (type, BISH[2]), *Forbes 190K* (A, BISH, UC).

2. **Hesperomannia arbuscula** Hillebrand

Hesperomannia arbuscula Hillebr., Fl. Hawaii. Is., 232, 1888.

Compared with *H. Lydgatei*, the remaining taxa are remarkably uniform. *Hesperomannia arbuscula* has been maintained as distinct here because of its geographical distribution and the constancy of the leaf shape and indument characters. In addition, the occurrence of slightly different plants on Oahu and West Maui respectively suggests that if the two populations are to be recognized as separate subspecifically, they are best grouped as a species separate from *H. arborescens*.

[2] Abbreviations of herbaria according to J. Lanjouw and F. A. Stafleu, Index Herbariorum, Part I, 1954, Utrecht.

2A. **Hesperomannia arbuscula** subsp. **arbuscula**

This taxon is known only from the type collection. Since repeated exploration of West Maui has failed to rediscover this plant, it may be extinct. Because the type at Berlin is apparently destroyed and the sterile type fragment at the Bishop Museum is inadequate, the isotype material in the Gray Herbarium remains the only usable material.

Representative specimens — West Maui: *Bishop, 1871* (type fragment, BISH; isotype, GH).

2B. ***Hesperomannia arbuscula*** subsp. ***oahuensis*** (Hillebr.) comb. nov.

Hesperomannia arborescens var. *oahuensis* Hillebr., Fl. Hawaii. Is., 232, 1888.

Hesperomannia oahuensis (Hillebr.) Degener, Flora Hawaiiensis. 1938.

Hesperomannia oahuensis, like the earlier variety of Hillebrand, was erected on the basis of material from Mt. Kaala, Oahu. Since Degener copied the description of *H. arbuscula* from that of Hillebrand, did not illustrate *H. arbuscula*, and cited the type only as "before 1888," it seems likely that Degener did not study the fertile specimens of *H. arbuscula* (mentioned above) extant at that time. Examination of both Oahu and Maui material reveals the small differences noted in the key above, but close identity in all other characters. Contrary to Degener's description of *H. oahuensis*, leaves with dentate margins may be found in this taxon.

Representative specimens—Oahu, Mt. Kaala and vicinity: *Hillebrand, 1871* (GH), *Degener and Salucop 11200* (BISH, GH).

3. **Hesperomannia arborescens** Gray

Hesperomannia arborescens Gray, Amer. Acad. Arts and Sci., Proc. 6: 554, 1886.

The type specimen of *H. arborescens* was collected on Lanai. Subsequent to Gray's description of this species, the first in the genus,

various authors have found difficulty in separating specimens collected later on Oahu from the Lanai material. Rock (1913: 507) and Skottsberg (1944: 512) find considerable similarity. Examination of the type specimens of all the taxa treated here as *H. arborescens*, as well as the numerous specimens which have been collected at various stations in the Koolau Mts., Oahu, reveals that considerable variability exists in this species. The descriptions of Degener for taxa in this group do not allow for this variability, as the comments below will indicate. The characters used by Degener in separating the species of this group have been found to have frequent exceptions and various degrees of intermediacy. For this reason the writer has found it inadvisable to maintain the species proposed by Degener.

3A. **Hesperomannia arborescens** subsp. **arborescens**

The Lanai population of *H. arborescens* has not been encountered since a single tree was seen in 1931, and may now be assumed to be extinct. It is only dubiously separable from Oahu material. As the type specimen and the collection *Munro 492* show, clusters of fewer heads, pubescent involucral bracts, and glandular trichomes on the achenes, thought by Degener to be characteristic only of Oahu plants, may be found in the Lanai material. The latter is maintained as a subspecies here because of its geographical isolation and seemingly slightly longer achenes, although it is possible that longer achenes may be found in future collections of mature Oahu material. The leaves do not match those of a particular Oahu population in that they combine a broad shape with a prominently toothed margin and are glabrous. These leaf characters, however, may all be found in Oahu plants.

Representative specimens—Lanai, near summit: *Mann and Brigham 357* (type and isotype, GH), *Hillebrand, 1874* (GH), *Munro 492* (A, BISH).

3B. ***Hesperomannia arborescens*** subsp. ***Bushiana*** (Degener) comb. nov.

Hesperomannia Bushiana Degener, Flora Hawaiiensis. 1933.

The small population found at the crest of Halawa ridge, Koolau Range, Oahu, is the most distinctive in the *H. arborescens* complex. The type specimen and the collection *Degener 11927a* show that the heads are uniformly solitary and smaller than in subsp. *Swezeyi*. The smaller head size, however, is not so pronounced as Degener's description indicates. Heads with as few as 30 flowers may be found in specimens of subsp. *Swezeyi* such as *Degener 10007; H. Bushiana* was described by Degener as having "approximately 25 flowers" per head. Solitary heads are occasional or frequent in populations treated here as subsp. *Swezeyi*. The combination of narrow leaves with toothed margins is not represented in other populations, but equally narrow leaves and leaves with toothed margins may be found independently in various localities, so the combination of these two characters in subsp. *Bushiana* is not surprising. In view of the closeness of this plant to some populations of subsp. *Swezeyi*, it has seemed preferable to recognize it as a subspecies in this complex, rather than a species coordinate with *H. arborescens*.

Representative specimens—Oahu, Koolau Range, Halawa: *Bush et al. 9981* (type, BISH), *Degener 11927a* (BISH).

3C. ***Hesperomannia arborescens*** subsp. ***Swezeyi*** (Degener) comb. nov.

Hesperomannia Swezeyi Degener, Flora Hawaiiensis. 1933.

Hesperomannia Bushiana var. *Fosbergii* Degener, Flora Hawaiiensis. 1937.

Within this subspecies are included all the populations of the Koolau Range except *H. arborescens* subsp. *Bushiana*. This group has been previously divided by Degener into *H. Swezeyi* and *H. Bushiana* var. *Fosbergii*. He

regards the latter as intermediate between *H. Swezeyi* and *H. Bushiana*. While this variety could be interpreted as being intermediate in number of heads per cluster, it has entire leaves, which are not characteristically found in either *H. Bushiana* or the plants regarded by Degener as *H. Swezeyi*. The type of *H. Swezeyi* is based upon material from the northern end of the Koolau Range. Other similar plants may be found midway along this range, in Kipapa and Halawa canyons, for example, as well as at the east end, on Mt. Konahuanui. While the type of *H. Bushiana* var. *Fosbergii* comes from the middle portion of the range (Kalauao ridge), plants which would have to be referred to this variety by virtue of limited numbers of heads and entire leaves may also be found at the north end of the range (e.g., *Fosberg 9419*), separated from the Kalauao populations by what could only be interpreted as *H. arborescens* subsp. *Swezeyi*. Thus, *H. Bushiana* var. *Fosbergii* has no geographical unity. Moreover, a number of specimens show intermediacy, as indicated below. It seems best to refer all the Koolau Mts. material except the extreme variant treated here as *H. arborescens* subsp. *Bushiana* to *H. arborescens* subsp. *Swezeyi*. *Hesperomannia arborescens* would seem to be an instance in which a species is broken up by the severe topography found in the Hawaiian Islands into small colonies in which various characters attain degrees of stabilization independently. Taxonomic recognition of portions of such a polymorphic complex does not seem advisable in most instances, since the essential continuity of the variation pattern is then lost.

Representative specimens—Oahu, Koolau Range. Specimens typical of "*H. Swezeyi*": Pupukea-Kahuku trail: *Degener and Swezey 4398* (type, BISH), *Degener and Shear 3397* (GH); Anahulu trail: *Degener et al. 10079* (BISH); S. Opaeula ridge: *Suehiro, Sept. 1933* (BISH); Kipapa trail: *Hosaka 619* (BISH), *Fosberg 9820* (BISH), *Degener et al. 10007* (BISH); Halawa trail: *Degener 11927* (BISH), *Carlquist H3* (BISH, UC); Mt. Konahuanui: *Rock 1910* (A), *Rock 1912* (GH). Specimens typical of "*H. Bushiana* var. *Fosbergii*": Laie-Waimea trail: *Fosberg et al. 9419* (BISH); Waimalu-Hanaiki trail: *Judd 1244* (BISH); Waimalu-Kalauao trail: *Fosberg 9470* (type, BISH). Specimens showing intermediacy between the above two types: Waimea ridge: *Forbes 2035.0* (BISH); Pupukea-Kahuku trail: *Degener 7445* (BISH), *Degener 7448* (BISH); Wahiawa gulches: *Forbes 1703.0* (BISH, UC).

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The Life History of the Polychaetous Annelid *Neanthes caudata* (delle Chiaje), Including a Summary of Development in the Family Nereidae[1]

DONALD J. REISH[2]

THE STUDY OF REPRODUCTION, development, and life history of the polychaete family Nereidae has attracted considerable attention in the past. Stimulus for this interest undoubtably is due, in part, to the world-wide distribution of the family, the phenomenon of epitoky (=heteronereis), and the diverse reproductive patterns. A total of 20 species of nereids has been studied in the past; information about them has been summarized in Table 1. Reproduction and development of *Neanthes caudata* have been studied previously by Herpin (1923, 1924, 1926) at Cherbourg, France. He reared this species through the 24-segmented stage.

This is the first report of the species in the Pacific Ocean. Fauvel (1923) stated that it inhabited muddy and sandy bottoms in Europe, and recently Day (1953) reported it from South Africa. The first specimens from the Pacific were encountered in a suspended sediment bottle collector (adapted from Thorson, 1946) which had been exposed for a 28 day interval in the West Basin of Los Angeles Harbor in November–December 1953. Quantitative bottom surveys of Los Angeles–Long Beach Harbors were made during August 1951 (Anon., 1952), and again in January 1954, but *N. caudata* was not taken. However, *N. caudata* was taken at many stations in both harbors in the surveys made in June and November 1954. It is believed to have been recently introduced into the harbor, possibly by ships.

MATERIALS AND METHODS

Culture Techniques

Living specimens were collected from sediment bottle collectors suspended for 28 days in the West Basin of Los Angeles Harbor. The techniques employed for culturing adults are in general similar to those utilized by the author for the adults of *Nereis grubei* (Kinberg) (Reish, 1953; 1954). Best results were obtained when the worms were placed in separate petri dishes. The worms were fed *Enteromorpha* sp., usually twice a week. This green alga was collected in quantities from estuaries in southern California. This alga was dried, and, prior to using, a small amount was soaked in sea water for a few minutes. Mud and sand, that had previously been dried, were substituted for *Enteromorpha* sp. with some success, but the use of the alga was

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favored because of the greater ease in observing the animal. The water in the petri dishes was changed at irregular intervals, usually once every two or three weeks.

Since the male incubates the fertilized eggs and larvae (Herpin, 1926), the developing worms were left undisturbed with the male until the larvae abandoned the parent tube. At this stage the larvae could be pipetted into separate petri dishes containing *Enteromorpha* sp. At first many larvae could be placed within the same dish, but as the worms grew they became cannibalistic and had to be separated.

A second method (Reish, 1953), but not as successful, was to place the bottom half of the petri dish containing a male and developing larvae into a one gallon aquarium. One liter of sea water was placed in the aquarium; the water was aerated by an aquarium stone connected to a compressed air system. Dried, ground *Enteromorpha* sp. was added twice a week. This technique was particularly useful for maintaining small larvae for a short period of time.

The Fighting Reaction

The sexes cannot be distinguished morphologically prior to the onset of sexual maturity. Females may be separated from immature females or males by the presence of developing ova in the coelom. Only by studying the reactions of sexually unknown specimens to known males or females could the males be distinguished. Herpin (1923; 1926) found that a female would readily accept a male but would fight off the introduction of a second female. These observations were confirmed by the author. Not only was it found that females would fight one another, but also a similar response occurred when two males were placed together. This behavior, which is termed the fighting reaction, is so definite that it was utilized to differentiate the sexes.

The fighting reaction is most pronounced when two worms of the same sex meet directly. Each proboscis is everted and the jaws extended to grasp the opposing animal. One such encounter lasts only a few seconds, but successive encounters may extend over an interval of several minutes. Termination of these fighting periods occurred when the worms became separated a few centimeters from one another. When one animal came in contact with any portion of the body of the second one other than its anterior end, it extended its jaws and attempted to grasp the worm. No injuries have been actually seen inflicted by this fighting, but when similar sized worms of the same sex were left together for a day, wounds were observed the next day. One or both of the animals lacked its posterior end, the remains of which appeared in fecal pellets. If the two worms were of the same sex but differed in size and were left together for a day, the larger worm usually will have eaten the smaller by the next day. This fighting reaction may account for the difficulty of culturing several worms within the same petri dish as discussed above.

A modification of this fighting reaction was observed in the male following egg-laying by the female. A male incubating eggs will frequently eat the spent female. A spent female will fight with a second female that has not yet laid her eggs. A male incubating eggs will fight with worms of either sex. After completion of the incubation period, the male will no longer fight with a female.

The basic behavior pattern appears to be an attraction to members of the opposite sex and a fighting reaction to members of the same sex. This pattern is altered in the male while incubating ova; he fights either sex. This behavior difference during the incubation period is apparently due to the presence of the eggs, although it was not the subject of any special investigation. Apparently there is no change in the behavior of the female during its life cycle.

Incubation of eggs is known to occur in *Micronereis variegata* (Rullier, 1954), *M. nanaimoensis* (Berkeley and Berkeley, 1953), *Platynereis massiliensis* (Hauenschild, 1951), *Laeonereis glauca* (Herpin, 1929), and *Cera-*

tonereis costae (Durchon, 1956), but it is not known whether or not this fighting reaction occurs in these species.

REPRODUCTION AND DEVELOPMENT

Sex Ratio

As reviewed by the author (1954), little is known concerning the sex ratio in the nereids. A ratio of one to one exists in *Nereis grubei* (Reish, 1954) on the basis of laboratory-reared specimens and field collections. Population studies showed a ratio of five males to four females in *Perinereis nuntia* var. *brevicirris* Grube (Takahasi, 1933), and 40 per cent males in *Nereis diversicolor* from South Baltic Sea (Bogucki, 1954) but only 10 per cent from the southern English coast (Dales, 1950).

Specimens of *N. caudata* were isolated into individual petri dishes shortly after they had left the parent tube. These worms were observed periodically for signs of egg formation. Those specimens which did not develop eggs were placed separately into a dish containing a female. The behavior of these worms was observed when they came in contact with one another. If the animals did not fight, then the unknown was considered a male. If the animals did fight, then the unknown was considered to be a female. The worms were then returned to separate petri dishes for further observations. No changes in the response to the fighting reaction were observed subsequently. A total of 170 specimens were isolated in this manner; they were offspring from six different matings. The results indicated a sex ratio of one to one; there were 88 females and 82 males.

Spawning

Spawning has never been observed in *N. caudata*. It has been described for several species of epitokal nereids (Reish, 1954) and in *Nereis diversicolor* (Bogucki, 1954). In *N. diversicolor*, a non-epitokal form, Bogucki found that the eggs are released through ruptures in the body wall, and that sperm may be discharged either through the nephridia or through ruptures in the body wall.

Some details concerning spawning behavior in *N. caudata* can be given, however. A series of 10 dishes, each containing a male and female, were observed at hourly intervals during the day (but not the week end) for a three-week period. Eight of the ten pairs spawned during the period. In one instance the female laid all her eggs between one hour observational periods. In a second instance a female was seen that had laid about one-half of her eggs. It is not known whether or not she was in the act of laying at the time of observation. She died three days later without laying any additional eggs. The remaining six pairs laid eggs either during the night or over the week end.

Freshly laid eggs of *N. caudata* were molded into a mucoid tube of one egg in thickness by the male. The male was undulating its body at all times. At first the eggs were free and easily withdrawn with a micropipette, but after the male had molded them into an egg tube, they became appressed and were difficult to remove with a micropipette. No gelatinous envelope (Hemplemann, 1911) surrounded the fertilization membrane as is typical for the epitokal nereids.

No sperm were observed in the water during placement of the eggs by the male. No dissections were made of these males. Periodic coelomic smears of the posterior part of known males did not reveal the presence of any bodies that could be definitely attributed to sperm or spermatic masses. Sperm was seen embedded within the space between the fertilization membrane and the developing ovum by Herpin (1926, fig. 115) and the author.

Fate of the Parents

Herpin (1923; 1926) stated that following completion of the larval incubation period, the male resumed its former life, and in one instance a male would reproduce a second time. The fate of the female was unknown except in one instance where Herpin noted

that the male had eaten the female the day following egg-laying.

The observations of Herpin were confirmed, and the following additional details can be given. The female either died after egg-laying or was eaten by the male. This cannibalistic action by the male is believed to be incidental because the fate of the female was approximately equally divided between the two causes. One female lived a total of six days following egg-laying, but this was exceptional. Typically the female lives two or three days after laying her eggs before dying. The females ate *Enteromorpha* sp. until a day before egg-laying, but none of them resumed feeding after spawning.

After the larvae have left the tube of the parent, the male may also abandon the tube, but not necessarily. The male may reproduce and incubate larvae more than once. Many males have fertilized and incubated eggs two times and one male has successfully incubated eggs three times in the laboratory. How soon after completion of one incubation period the male can reproduce with a second female was not completely ascertained because of the lack of mature females at the critical time. The shortest period of time between two fertilization periods for one male was 27 days. The first eggs were fertilized on September 12, 1954, with all the larvae leaving the tube by September 22, 1954. The second female was placed with the male on October 4, 1954, with fertilization occurring October 8, 1954. *Neanthes caudata* is the only dioecious species of nereid known in which at least one of the sexes can reproduce a second time.

Number of Eggs

Little information on the number of eggs or larvae of nereids has been recorded in the literature. Smith (1950) stated that *Neanthes lighti* produced several hundred eggs but only 80 to 100 larvae were released. Rullier (1954) found that *Micronereis variegata* laid from 20 to 80 eggs in a gelatinous matrix. In *Nereis grubei* the author (unpublished data) found the number of eggs to vary from 1,000 to 49,000. The lower figures were generally for those animals reared in the laboratory, and the higher figures were from animals collected from nature.

The number of larvae of *N. caudata* hatching from the parent tube were counted rather than the eggs because of the greater ease in counting. This figure is believed to represent a close approximation of the actual number of eggs laid by the female since non-developing eggs were not seen. Only one count of larvae was made from a female collected from nature; a total of 481 larvae left the parent tube. Counts for seven laboratory-reared females ranged from 143 to 791, with a median of 365 larvae.

Fertilization and Early Development

The unfertilized ovum of *Neanthes caudata* is spherical and yellow (Fig. 1). Eggs from laboratory-reared females measured from 420 to 520 μ in diameter. The ova observed by Herpin (1926) were 600 μ in diameter, the largest size recorded for a nereid egg. No distinct cortical layer was observed.

The process of fertilization has not been observed either by Herpin or by the author. Eggs that had been laid within an hour al-

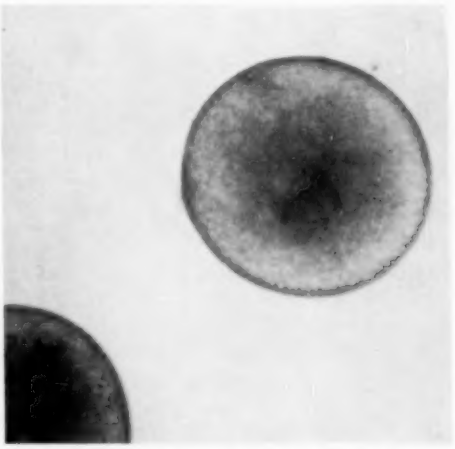

FIG. 1. Photomicrograph of an unfertilized egg of *Neanthes caudata*. Diameter, 425 μ.

ready possessed fertilization membranes. As stated above, sperm were observed embedded in the space within the fertilization membrane. Cleavage proceeded very slowly through the eight-cell stage. The cleavage pattern was spiral and similar to that described by E. B. Wilson (1892) for *Neanthes succinea* and *Platynereis dumerilii*. However, there was no further cleavage of the four yolky macromeres beyond this stage of development. These yolk cells will eventually become enclosed within the digestive tract and will be utilized for food (Figs. 2 to 7). These four cells can be seen until just prior to feeding.

Cleavage beyond the eight-cell stage was limited to the animal pole (Fig. 2, arrow). These cells come to surround the four macromeres by epibolic growth. The embryo was never ciliated, which is unique among the nereids.

The developing egg remained spherical until the seventh day when a slight elongation of the embryo was noted (Fig. 3). Longitudinal muscular movement appeared at this time. The course of growth from the elongation of the embryo through sexual maturity has been summarized in Table 2. Formation

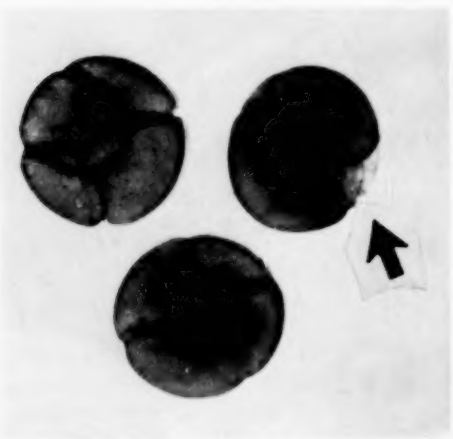

FIG. 2. Photomicrograph of developing embryos of about 18 hours in age showing the four macromeres. Arrow indicates site of cleaving micromeres. Diameter, 520 μ.

FIG. 3. Photomicrograph of an elongating embryo of seven days in age encased in egg capsule. Length, 520 μ.

of the three larval segments occurred at eight days. The anal cirri appeared as knobs at this time, but there were no indications of cephalic appendages (Fig. 4). Shortly thereafter the larvae hatched from the egg capsule.

During the ninth day the fourth larval setigerous segment, the first pair of peristomial tentacles, and the tentacles appeared. In addition, as many as four presumptive segments were often discernible as simple protuberances (Figs. 5 to 7). The four yolk-cells were still present, and because of their large size, they gave a humpback appearance to the larvae (Fig. 5). New segments were added rapidly until the animal had developed about 16 segments at 16 days (Figs. 5 to 8). The young worms, which have been crawling actively within the parent tube, begin to abandon the tube in the next few days. The larvae crawl about the petri dish, construct mucoid tubes, and begin to feed upon *Enteromorpha* sp. by 21 days. There is no true planktonic stage in *N. caudata*. However, if the young animals are disturbed, they abandon their tube and either crawl or swim away. This behavior may play an important role in the distribution of *N. caudata*, particularly within a bay or

harbor. One specimen with 18 setigerous segments was taken in a plankton tow on October 21, 1954, in Los Angeles inner harbor. Further appearance of segments is indicated in Table 2.

The tentacles and first pair of peristomial tentacles appear as small knobs on the ninth day. The next two pairs of peristomial tentacles arise in the next two days (Fig. 5). The fourth pair was slow to appear; it did not form until the larva was 23 days of age and possessed 24 segments. The palpi were seen first at 10 days (Fig. 5) and became biarticulated a few days later.

The jaws were noticed when the larvae were 10 days old. They were colorless structures and consisted of only the terminal tooth. The first lateral tooth was added by the next day. Additional lateral teeth were formed rapidly; a larva 21 days old had 7 teeth. The tips of the jaws became dark brown at this time. Lateral movements of the jaws did not occur until the larvae had 15 segments, or just prior to leaving the parent tube.

Paragnaths were seen first on the maxillary ring at 14 days; they did not appear on the oral ring until 21 days. The paragnaths became dark brown at about 26 days when the animals possessed 32 segments. Figure 9 is a photomicrograph of the paragnaths of area I. A total of 37 paragnaths was observed in this specimen, which was a typical number for young worms. Adult worms reared in the laboratory had from 12 to 16 paragnaths present, indicating a loss in number with age. This was contrary to what was observed by the author (1954) in *Nereis grubei*, which showed little change, if any, with age.

FIG. 4. Photomicrograph of a three-segmented larva of eight days in age. The anal cirri are beginning to develop as small knobs at the right side of the figure. Length, 750 μ.

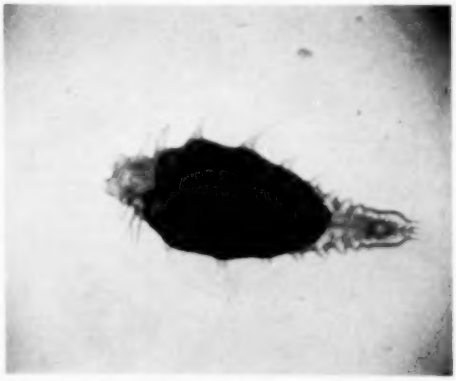

FIG. 5. Photomicrograph of five-setigerous segmented larva 10 days old. Shown in formation (from left to right) are the tentacles, palpi, two pairs of peristomial tentacles, five setigerous segments, four segments without setae, and one pair of anal cirri. Length, 1.1 mm.

The development of *N. caudata* collected at Cherbourg, France (Herpin, 1926), and Los Angeles Harbor, California, does not differ in morphological details, only in regard to time of appearance of structures. The three larval setigerous segments arose a day earlier at Cherbourg. This difference in one day continued until about 10 to 11 days when larvae from both localities possessed six larval segments. However, in the Los Angeles Harbor

FIG. 6. Photomicrograph of seven-setigerous segmented larva 11 days old. Appendages as in Figure 5. Note the humpback appearance of the animals in Figures 5 and 6. Length, 1.1 mm.

material the 20-segmented stage was attained about eight days before the Cherbourg population.

Later Stages of Growth

Growth in the later stages of development in the nereids has been measured in three different ways. The use of segment number per unit of time has been employed most frequently (Banse, 1954; Bogucki, 1954; Dales, 1950; Hauenschild, 1951; Hemplemann, 1911; Herpin, 1926; Rullier, 1954; and D. P. Wilson, 1932). Body length was utilized by Bogucki (1954), Dales (1951), and Smidt (1951). The weight of the animal was determined periodically and correlated with metamorphosis and the appearance of genital products in *Nereis grubei* by the author (1954). With the former two methods, a sigmoid curve for growth was obtained. Similar results were attained for *N. grubei* when the number of segments per unit time was plotted (Fig. 8) using the data given by Reish (1954).

Growth in *Neanthes caudata* was followed by determining the number of segments present per unit time; the results have been summarized in Table 1 and plotted in Figure 8. The data are based on the growth of the offspring of one mating. Observations upon living specimens are difficult to make since they move about continually within their tube. The activity of these animals was slowed by placing the petri dish within an ice bath.

It is readily observable that growth in *N. caudata* differs from *Nereis grubei*. The appearance of the three larval setigerous segments lags in *N. caudata*, but the attainment of additional segments in *N. caudata* soon surpasses *Nereis grubei*. However, a plateau is reached at the time the larvae of *N. caudata* leave the parent tube and commence feeding at the 17- to 19-setigerous segment stage (Fig. 8; Table 1). Shortly thereafter a second growth spurt occurs which continued until the eggs were first discernible in the females at around the 55-segment stage. A few additional segments were added during the next 10 to 15 days. The maximum number of

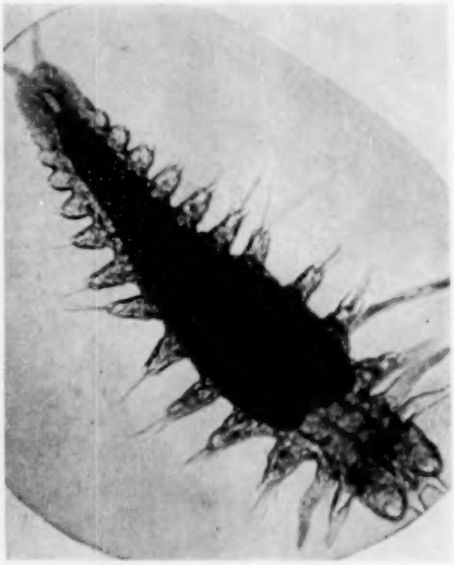

FIG. 7. Photomicrograph of eight-setigerous segmented larva 12 days old. Appendages as in Figure 5. Length, 1.2 mm.

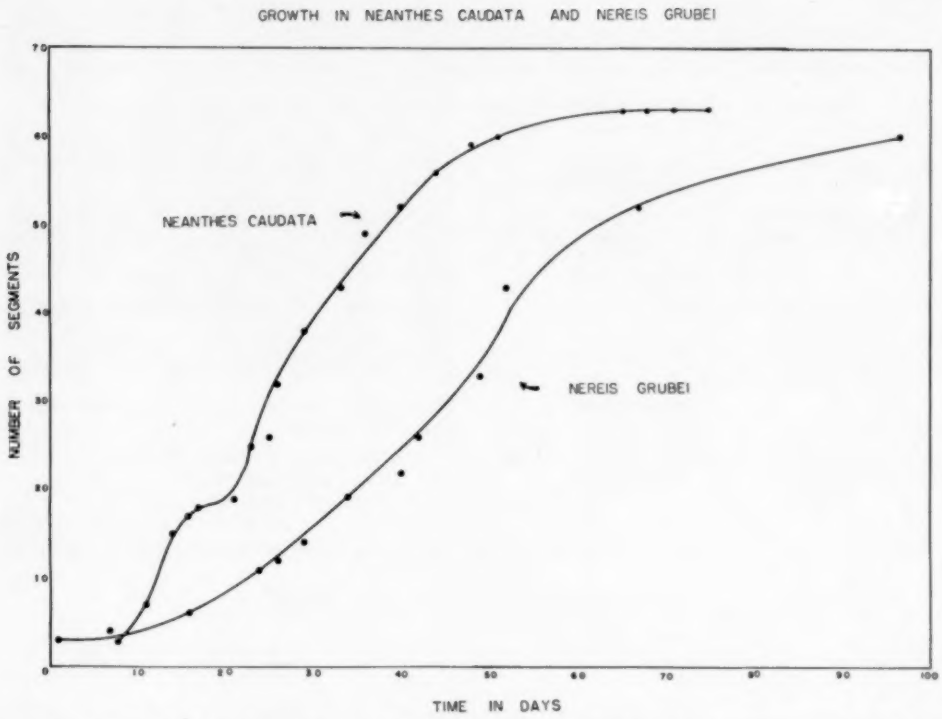

FIG. 8. Growth in *Neanthes caudata* and *Nereis grubei* as measured by the number of segments per unit time. Data for *Nereis grubei* taken from Reish (1954: 16).

segments were attained about 10 days before spawning. No sexual differences were noted with regard to the appearance or number of segments, and there was no indication that the males increase their number of segments between their first and second reproductive periods.

So far as is known, there seem to be two types of growth curves in the nereids when the appearance of segments is used as the unit of measurement. *Neanthes caudata* possesses a sigmoid growth curve with an interrupted plateau occurring at the onset of feeding. There is no initial prolonged phase after the appearance of the three larval segments in *N. caudata*, as is typical for the majority of nereids. It is possible that *N. lighti* is characterized by an interrupted growth curve. A similar initial spurt as in *N. caudata* was found when the data from Smith (1950) was plotted. Development of *N. lighti* was not followed after birth by Smith. As summarized in Table 1, several nereids incubate their young, but either data were not included or development was not continued far enough to ascertain whether or not these species possess a growth curve similar to *N. caudata*.

Sexual maturity was reached in 65 days (Table 2) with the female laying her eggs, and the male incubating them. The F_2 generation reproduced 148 days later, and the F_3 generation reproduced 203 days later. Five generations have completed their life cycle in the laboratory within a period of one year. No gross morphological differences between the different matings or generations were

TABLE 1

REVIEW OF REPRODUCTION AND DEVELOPMENT IN FAMILY NEREIDAE

SPECIES	METHOD OF REPRODUCTION	MAXIMUM STAGE REARED	REFERENCE
Ceratonereis costae (Grube)	Eggs laid in jelly mass in tube; eggs incubated by ♀	37 day old larva had 6 larval segments	Durchon, 1956
Micronereis nanaimoensis Berkeley and Berkeley	Swarming and pairing but not epitokal; eggs laid in jelly mass with ♂ incubating	23 day old larvae possessed 3 larval segments	Berkeley and Berkeley, 1953
M. variegata Claparède	As *M. nanaimoensis*	40 day old larvae possessed 6 segments	Rullier, 1954
Namanereis indica (Southern)	Protandric hermaphrodite	Preliminary note only	Aiyar, 1935
N. raneuensis (Feuerborn)	Hermaphroditic	4 day old larva possessed 3 larval segments	Feuerborn, 1932
Neanthes caudata (delle Chiaje)	Eggs laid in tube; eggs incubated by ♂	Sexual maturity in 2 months; ♂ reproduced more than once; ♀ reproduced only once	Reported herein
N. japonica (Izuka)	Swarming but not epitokal	9 day old larva had 4 larval segments	Izuka, 1908; 1912
N. lighti Hartman	Viviparity and probably self-fertilizing hermaphrodite	Parturation occurred at 3–4 weeks of larvae with up to 30 segments	Smith, 1950
N. succinea (Frey and Leuckart)	Epitoky	60 day old larva had 17 segments	Banse, 1954
Nereis diversicolor Müller	Direct; population 40% ♂ in Baltic Sea and 10% ♂ on English coast	Sexual maturity reached in 10 months	Bogucki, 1954; Dales, 1950
N. grubei (Kinberg)	Epitoky	Sexual maturity in 3.5 months; offspring all epitokal	Reish, 1954
N. irrorata (Malmgren)	Epitoky	3 larval segments	Herpin, 1926
N. pelagica Linnaeus	Epitoky	One year old specimen had 60 segments	D. P. Wilson, 1932
N. procera Ehlers	Epitoky	Reared to sexual maturity but no details given	Guberlet, 1934*b*
N. vexillosa Grube	Epitoky; eggs laid in jelly mass; no incubation	One specimen was 13 months old but not sexually mature at time of death	Johnson, 1943
Perinereis cultrifera (Grube)	Epitoky	45 day old larva had 7 segments	Herpin, 1926
P. marioni (Audouin and Milne-Edwards)	Epitoky	80 day old larva had 19 segments	Herpin, 1926
Platynereis bicanaliculata (Baird)	Epitoky	Sexual maturity in 9 months; offspring all epitokal	Guberlet, 1934*a*
P. dumerilii (Audouin and Milne-Edwards)	Epitoky	Sexual maturity in 21 weeks; offspring all epitokal	Hauenschild, 1951
P. massiliensis (Moquin-Tandon)	Protandric hermaphrodite; ♂ incubates eggs	Sexual maturity; sperm present when worm had 17–25 segments; eggs present when worm had 41–47 segments	Hauenschild, 1951

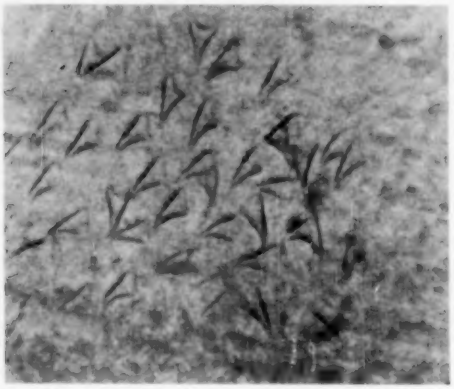

FIG. 9. Photomicrograph of colorless paragnaths on area I of a 17-segmented worm 17 days old. Dimensions top to bottom of area I, 70 μ.

noted; however, a statistical analysis of the offspring was not the subject of any special study.

DISCUSSION

A review of the literature on nereid development (summarized in Table 1, which gives the method of reproduction, the maximum stage to which the species has been reared, and the most recent reference) shows many different reproductive methods but apparently only two patterns of development. The most common method of reproduction is through epitoky. In this method the worms abandon their tubes or burrows at maturity and the sexual elements are emptied directly into the water, where fertilization and development ensue. These ova give rise to planktogenic larvae (Hemplemann, 1911). Both male and female die after spawning. This form of reproduction has been observed and studied in *Neanthes succinea*, *Nereis grubei*, *N. irrorata*, *N. pelagica*, *N. procera*, *N. vexillosa*, *Perinereis cultrifera*, *P. marioni*, *Platynereis bicanaliculata*, and *P. dumerilii*. *Nereis vexillosa* deviates slightly from the pattern in that the eggs are laid in a gelatinous egg mass, rather than singly.

Swarming, without epitoky, followed by pairing and egg-laying, has been observed in *Micronereis variegata*, *M. nanaimoensis*, and *Neanthes japonica*. In the two species of *Micronereis*, the female lays the eggs in a gelatinous mass on the substrate and incubates them until the larvae emerge from the matrix. Fertilization takes place in the water mass in *N. japonica*.

The female of *Ceratonereis costae* lays her eggs in a gelatinous matrix within her tube. Neither epitoky nor swarming precedes egg-

TABLE 2
SEQUENCE OF EVENTS IN THE LIFE HISTORY OF *Neanthes caudata*

AGE IN DAYS	CHARACTERISTICS
7	Elongation of egg; muscular movement; length 0.52 mm.
8	Appearance of three larval segments; anal cirri; hatching from egg capsule; length 0.62 mm.
9	Four larval segments; tentacles; one pair of peristomial tentacles; length 1.0 mm.
10	Five larval segments; two pairs of peristomial tentacles; early palpi; jaws with terminal tooth only; length 1.1 mm.
11	Seven larval segments; three pairs of peristomial tentacles.
13	Animals with 12 adult segments; setae of first larval segment drop out, segment becomes peristomium; jaws with four lateral teeth; length 1.4 mm.
14	Animals with 14 segments; jaws with five lateral teeth; paragnaths on maxillary ring only.
16	Animals with 16 segments; jaws with six lateral teeth.
21	Animals with 18 segments; jaws with seven lateral teeth; jaws becoming dark brown at tips; paragnaths present on oral ring; worms have left parent tube and have built own mucoid tube; length 4.0 mm.
23	Animals with 24 segments; four pairs of peristomial tentacles; feeding; length 6.0 mm.
26	Animals with 32 segments; paragnaths getting dark brown.
33	Animals with 42 segments.
36	Animals with 48 segments.
40	Animals with 51 segments.
44	Animals with 55 segments; eggs observed in coelom.
65	Female lays eggs with male incubating.
92	Male fertilized eggs from second female.
148	F_2 generation reproduced.
203	F_3 generation reproduced.

laying in the population in Algeria. The eggs are incubated by the female (Durchon, 1956).

The larvae of *Nereis diversicolor* and *Neanthes lighti* resemble those species given above, but differ in their site of development. This proceeds on the substrate in *N. diversicolor* (Dales, 1950) and in the coelom of viviparous *N. lighti* (Smith, 1950).

Only two of the species studied have eggs with a large amount of yolk, giving rise to nereidogenic larvae. In both of these species, the male incubates the eggs within a mucoid tube, a ciliated embryonic stage is lacking, there is no larval planktonic stage, and the adults do not undergo metamorphosis into epitoky prior to sexual maturity. One of these two species, *Platynereis massiliensis*, has been studied by Hauenschild (1951) who found it to be a protandric hermaphrodite. The other is *Neanthes caudata*, whose life history is discussed in this paper.

It certainly appears from this summary that the method of reproduction and development of *Neanthes caudata* is unusual among the nereids. But only a few species have been studied and there is too little information available as yet to make any positive statement on this subject. As no correlation is apparent between genera and mode of reproduction, the life history of each species must be worked out before any authoritative conclusions can be reached.

SUMMARY

1. Reproduction and development in the polychaete family Nereidae was reviewed and summarized in Table. 1.
2. *Neanthes caudata* was reported from the Pacific Ocean for the first time. It was taken from suspended sediment bottle collectors and from the bottom of Los Angeles–Long Beach Harbors.
3. Techniques for rearing *N. caudata* through sexual maturity were described.
4. Males and females are attracted to one another, whereas individuals of the same sex fight with one another. This behavior is altered in the male while he is incubating the developing ova; he fights either sex.
5. A sex ratio of one to one was found in laboratory-reared specimens.
6. Spawning was not seen. The female died or was eaten by the male following egg-laying. The male incubated the eggs within its mucoid tube. The male may reproduce more than once.
7. The ova ranged in size from 420 to 520 μ in diameter. Fertilization was not observed. Cleavage proceeded very slowly. The four macromeres did not undergo further cleavage beyond the eight-cell stage. The micromeres continued to divide and gradually surrounded the macromeres by epibolic growth. The embryo was not ciliated. The three larval segments with setae appeared at eight days. The larvae left the parent tube at 21 days. Feeding commenced shortly thereafter. Sexual maturity was reached in both sexes in 65 days. The F_2 generation reproduced 83 days later and the F_3 generation 65 days later still. The sequence in the life history was summarized in Table 2.
8. *Neanthes caudata* was characterized by a sigmoid growth curve with an interrupted plateau, when the number of segments was used as a measure of growth. The interrupted plateau was correlated with the onset of feeding.

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Records of Bioluminescence in the Ocean[1]

BRIAN P. BODEN and ELIZABETH M. KAMPA[2]

DURING THE MONTH of June, 1955, while measurements were being made of the depth of penetration of moonlight into the sea off the Kona Coast (S. W. coast) of the island of Oahu in the Hawaiian group, some information was obtained on bioluminescence in deep water in this region and on the effect of moonlight on the vertical distribution of luminescent organisms. Observations of bioluminescence were also made off San Diego, California, during the month of January, 1956.

An underwater photometer (Kampa, 1955; Snodgrass *et al.*, 1957 in press) designed for work in the deep sonic-scattering layers was used for these measurements. This was equipped with a depth-indicator (Boden *et al.*, 1955) so that a precise knowledge of the depth of the instrument was available at all times. The instrument utilizes a 931-A photomultiplier tube oriented with the sensitive surface facing up. In front of this is a collimating tube at the base of which is a filter-holder for interference filters. The collimator ensures that the 5° useful angle of the filters is not exceeded. At the distal end of this tube is a diffusing plastic disc, which is a true Lambert-type collector—that is, under a uniform sky the intensity (I_θ) collected from the direction Θ would be

$$I_\theta = I_0 \cos \Theta.$$

Thus the instrument measures irradiance. The collimating tube and filter-holder are free-flooding. The dark-current level of the instrument changes less than 0.2 millivolts on the 0–10 millivolt recorder range through the temperature range 10–30°C. It fluctuates about 0.03 millivolts at any particular temperature. The instrument registers down to 1×10^{-6} μ watts/cm^2.

Observations of bioluminescence in surface waters were made off San Diego (Lat. 32° 38′ N., Long. 117° 35′ W.) on the morning of January 18, 1956.

The photometer was lowered with its sensitive surface pointed downward. The sky was cloudless and moonless, and the first cast was made immediately before the beginning of official twilight. Luminescence was clearly visible at the surface at this time, and porpoises were seen to leave bright trails of light in their wakes.

Flashes, or bursts of light, were observed by the instrument, and recorded on a Leeds and Northrup Speedomax recorder, from the surface to a depth of 60 meters. From a depth of about 25 meters downward the flashes were superimposed on the dark-current level of

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[2] Scripps Institution of Oceanography, University of California, La Jolla, California. Manuscript received February 27, 1956.

the instrument, and at times apparently single flashes reached a level of 2×10^{-3} μ watts/cm^2.

A later cast, with the photometer still pointed downward, revealed that at sunrise (0652 hrs.) the flashes were first recorded at a depth of about 110 meters.[3] All facts known to us indicate that these flashes are generated *in situ* and we interpret them as due to luminescent organisms, possibly both nekton and plankton.

Records of bioluminescence at depth were first made in Hawaii at midnight on the night of June 9, 1955. The moon, three days past the full, had just appeared over the mountains. Its angle of elevation at 2400 hours was 19°. The instrument was lowered without color filters, and total irradiance, as seen by the instrument, was recorded. The sky was partly cloudy, but the moon remained clear throughout the observations.

Figure 1 is a tracing of the actual recording made on the Leeds and Northrup Speedomax recorder. Total irradiance (H) at any depth was obtained from

$$n = k\,H = \int_0^\infty E\,S\,d\,\lambda,$$

where n = recorder reading, E = energy of the source through the wave-length interval $d\,\lambda$, S = relative spectral sensitivity of the photomultiplier tube through the wave-length interval, $d\,\lambda$ (300–700 mμ). The value of k was obtained by calibration of the entire instrument against a Bureau of Standards source. The inset shows the relative spectral sensitivity of the 931-A tube used.

The dark-current level of the photometer was reached at 200 meters. From about 50 meters downward numerous brilliant flashes of light were recorded.

At some depths, for example 120–130 meters and 150–170 meters, the background light level appears to have remained constant or to have increased rather than to have decreased with depth.

Many types of luminescent marine animals, e.g., euphausiids, generate a steady glow of light for limited periods in contrast with the discrete flashes produced by others (Harvey, 1940). Possibly the sustained light level (Fig. 1) on which the flashes are superimposed at depths of 120–130 meters and 150–170 meters was due to a background glow produced by concentrations of such types, or by numerous flashes at varying distances.

An alternative explanation of the flashes can be found by visualizing a distribution of steadily-glowing organisms similar to that of stars in the sky, and a flashlike increase in the level of light due simply to the instrument's approach to and retreat from a glow during its descent. The rate of descent of the instrument was about 32 meters/minute. For this to be the true explanation, the glows would have had to be about 1 meter of depth apart, for the frequency of the flashes was about 36/minute.

Many luminescent organisms flash brightly when irritated mechanically or chemically. It is impossible at present to determine whether the observed flashes were due to spontaneous luminescence or whether the luminescence was intensified by agitation of the animals by the instrument.

Four more casts were made, using narrow-band interference filters, during the forty-five minutes after midnight. The angle of eleva-

[3] The possibility that these are artifacts due to instrument failure is to be considered. It is improbable that distortion due to pressure affected the circuitry, for the phenomenon was not observed when the instrument had been lowered to greater depths during daylight. It is improbable, too, that the effect could have been caused by water leakage, for moisture in the system has been shown to raise the dark current to such a high level that the recorder is immediately sent off scale. Furthermore the fact that color filters placed in the light-path reduced the amplitude of recorded flashes discounts the possibility that loose electrical connections were responsible. Another photometer, similar to the one employed here, has since shown that the flashes are not recorded when the sensitive element is covered but are when it is exposed immediately afterward at the same depth. Thus we believe that the instrument was sensing real light flashes.

Flashes of this nature could not have been caused by tilt of the instrument since it was pointed downward.

tion of the moon varied between 21° and 31° during this period. The interference filters employed were G. A. B. filters, manufactured in Liechtenstein, with half-peak band widths of about 10 mμ. Block filters are incorporated to reduce stray light and eliminate secondary transmission peaks. Peak transmissions, measured by a Beckman Model DU spectrophotom-

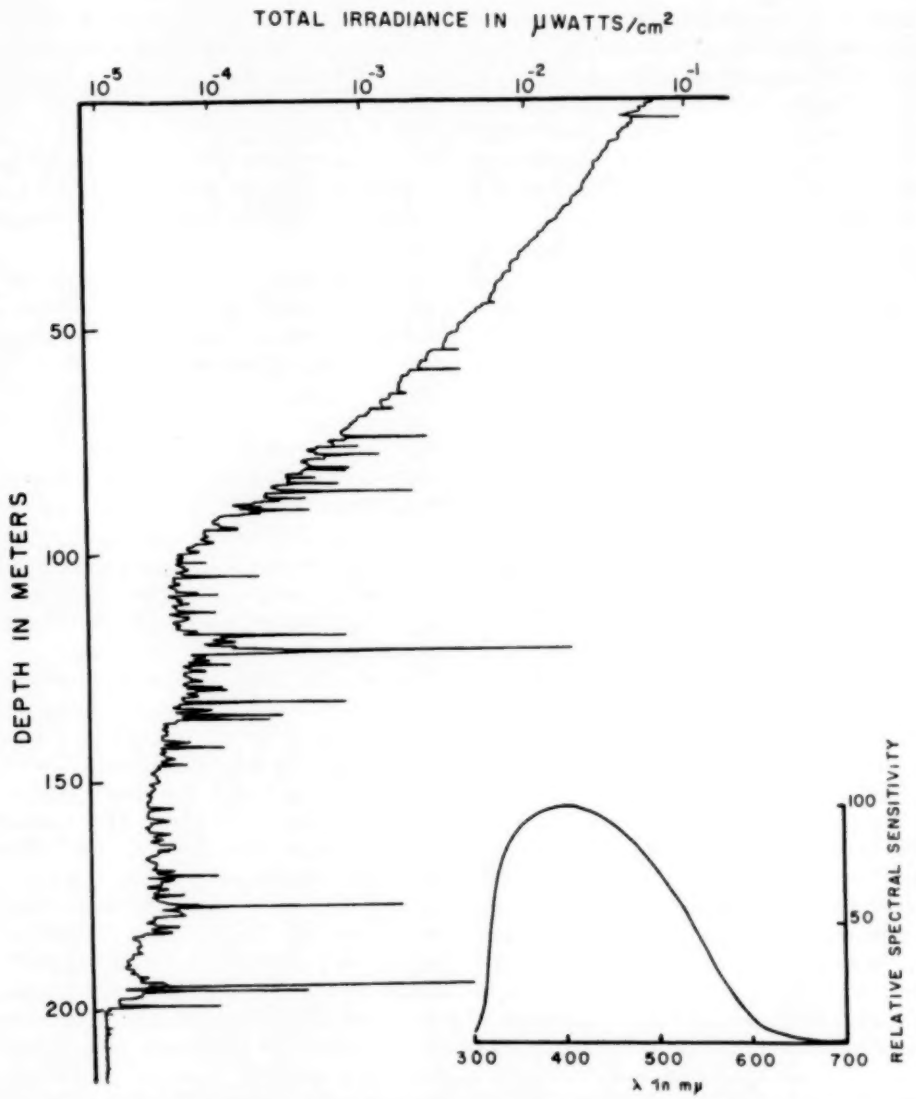

FIG. 1. Tracing of total irradiance recorded on Leeds and Northrup Speedomax recorder by bathyphotometer without color filters. Spectral sensitivity of the 931-A photomultiplier tube is shown in inset. This is from manufacturer's specifications and is an average curve. The record was made at 2400 hours, June 9, southwest of Oahu.

eter, are at 418, 491, 552, and 630 mμ (see inserts in Fig. 2).

Irradiance (H) was obtained from

$$n = k H = \int E T_f S d\lambda,$$

where n = recorder reading, E = energy of the source through the wave-length interval $d\lambda$, T_f = measured transmission of the individual interference filter through the wave-length interval $d\lambda$, and S = the relative sensitivity of the photomultiplier tube through the wave-length interval $d\lambda$. The value of k was obtained as indicated above.

Tracings of the recordings are shown in Figure 2. Orange light (λ max, 630 mμ) is seen to cut out at 11 meters, and no flashes are apparent. With the 418 mμ filter, the dark-current level of the instrument was reached at a depth of 280 meters.

The 418 mμ cast reveals an actual increase in irradiance with depth between 100 and 220 meters. Sudden flashes again occurred between 100 and 280 meters, but these, as recorded, were of lower amplitude than those in the unfiltered cast, presumably because of the narrowness and reduced intensity of the transmitted band.

These observations indicate that the light generated at depth is blue-violet (see Harvey, 1940, for spectral distribution of bioluminescence). It can be seen too (Fig. 2) that the flashes produced in the surface layers are greener.

The greater depth attained with a 418 mμ filter in the instrument (cf. Figs. 1 and 2) and the deeper flashes may be explained on the assumption that some of the light-generating constituents of the population had by then sought greater depths as the moon cleared the mountains and approached its zenith. The possibility that these constituents comprise a photoregulated community similar to the Californian deep-scattering layer may be inferred from this assumed downward migration with increasing illumination.

This inference is substantiated by observations made off San Diego (Lat. 32° 38′ N., Long. 117° 35′ W.) on January 17, 1956. At this time EDO fathograms and light measurements were made simultaneously during the periods of the twilight migration of the sonic-scattering layer. Figure 3A (1640–1650 hours) shows that flashes were first recorded as the photometer reached the depth of the scattering layer. Thirty minutes later (1720–1728 hours) the top of the scattering layer had reached a depth of 120 meters. Figure 3B shows that the first flashes recorded by the photometer were now at this same depth. On the day of these observations sunset was at 1706 hours.

We have recorded flashes, during our scattering-layer studies, in the Pacific, Atlantic and Mediterranean. They appear to increase both in frequency and amplitude during the twilight migration of the layer and at night. On this account it is extremely difficult to obtain an accurate picture of the spectral distribution of moonlight in the sea, or even of sunlight at scattering-layer depths.

Since the completion of this paper we have heard from Professor George L. Clarke of Harvard University (Clarke and Backus, in preparation) that he too has recorded flashes of luminescence off the Florida coast.

This phase of work on the sonic-scattering layers received additional support from the National Science Foundation and the Pauley Fund of the University of California. The inquiry was pursued from the Marine Laboratory of the University of Hawaii. The Californian data were obtained from the "USS EPCE(R) 855." Acknowledgment is made of the generous loan of the Research Vessel "Makua" by Mr. Vernon Brock, Director of the Territorial Fish and Game Commission, Hawaii. The U. S. Air Force and Marine Corps were unstinting in their loan of equipment and facilities. Data were analyzed and most of this paper was written at The Laboratory, Plymouth, England. The hospitality of the director, Mr. F. S. Russell, F. R. S., is most gratefully acknowledged. Professors

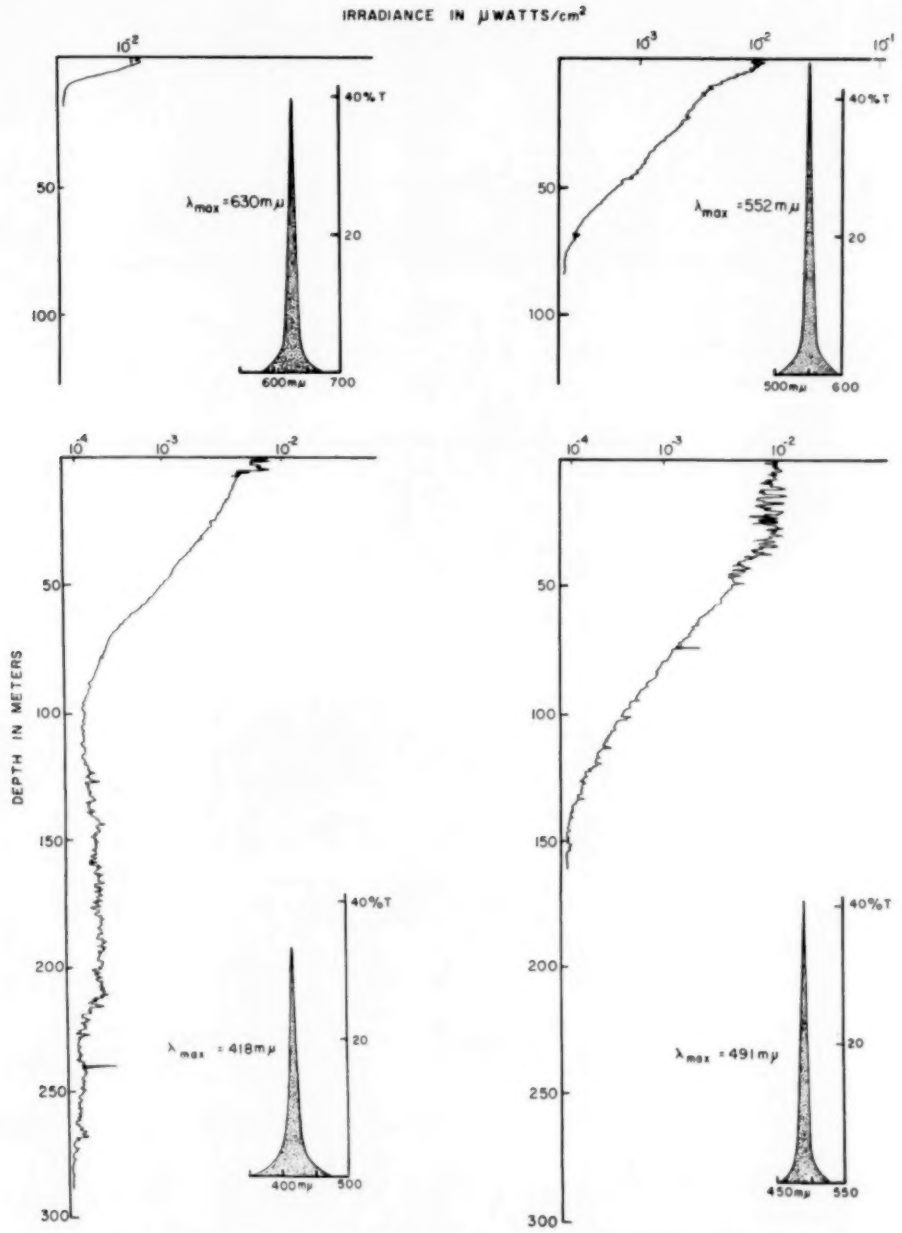

FIG. 2. Tracings of irradiance record at four different wave lengths as determined by bathyphotometer using interference filters. Insets show measured transmission curves of filters used. The records were made at the following times: 630 mμ—0020 hrs.; 552 mμ—0030 hrs.; 491 mμ—0044 hrs.; 418 mμ—0058 hrs.; all on June 10, southwest of Oahu.

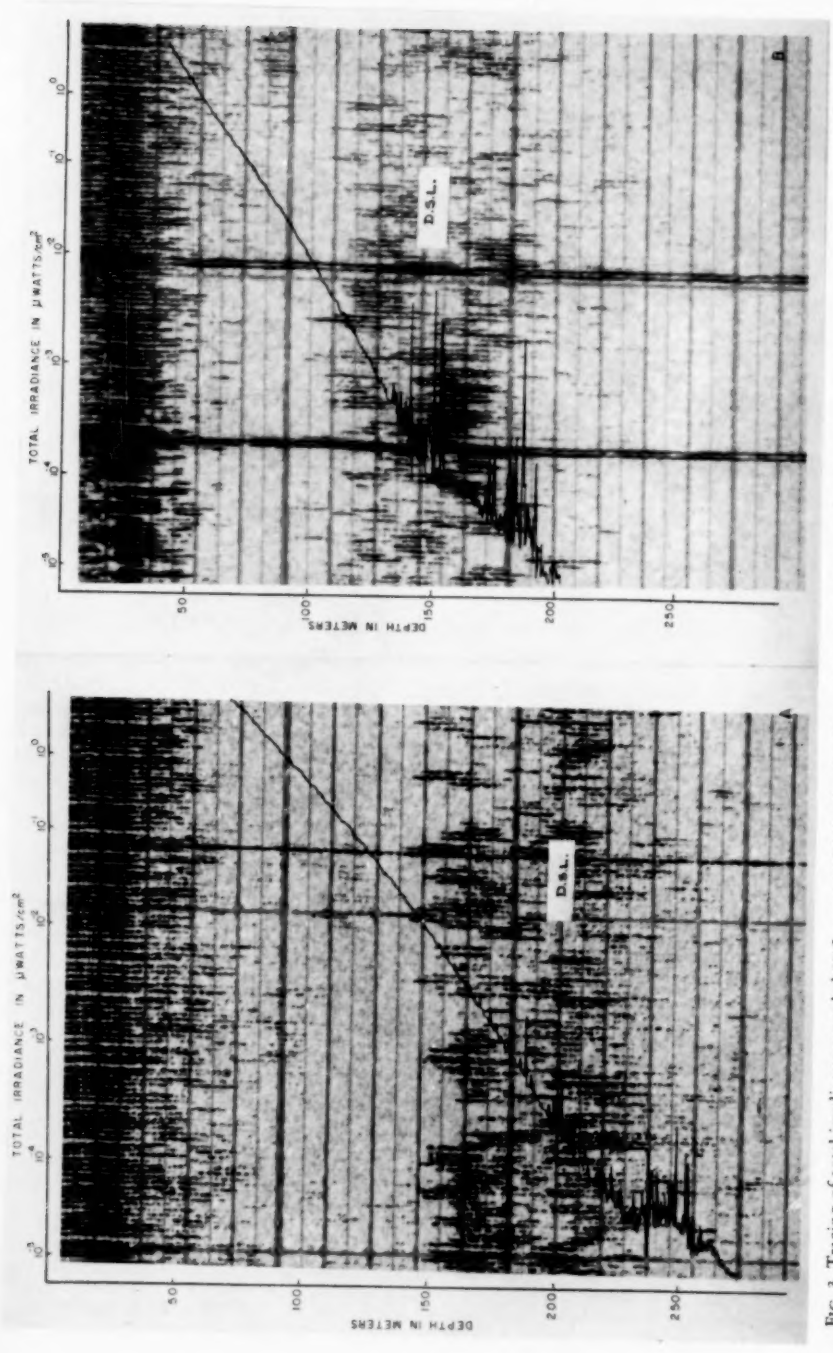

FIG. 3. Tracing of total irradiance recorded 17 January 1956, in the San Diego Trough, Latitude: 32° 38' North; Longitude: 117° 35' West. The superimposed fathograms were recorded at the same time. A: 1640–1650 hrs., B: 1720–1728 hrs. The light curve does not reach the surface because the upper limit of the photometer's range is about 2μ watts/cm².

Carl Eckart and Carl L. Hubbs of the Scripps Institution and Mr. John Tyler of the Visibility Laboratory of the Scripps Institution subjected the manuscript to vigorous and stimulating criticism.

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New Species and Records of Hawaiian Sponges

M. W. DE LAUBENFELS[1]

THREE PREVIOUS PAPERS on Hawaiian shallow-water sponges have appeared in *Pacific Science* (de Laubenfels, 1950, 1951, 1954). Repetition is here avoided, and it is assumed that the reader has consulted the earlier articles, especially that of 1950, on the sponges of Kaneohe Bay, Oahu. All of the sponges that are common about Oahu are described and named in that paper, and the key that is given there should be adequate. Further keys are inappropriate, because it is clear that almost any conceivable kind of sponge may be discovered in the next dredge haul. The present paper is based on three years' study, but it should be emphasized that even during the third year additional species were easily found.

Few references to the sponges of Oahu occur in the literature. Dr. C. H. Edmondson of the B. P. Bishop Museum in Honolulu has published (1946) on the reproduction of *Tethya*, but this is not a faunal paper. Casual references to sponges from Oahu occur, as discussed below, in some writings of Lendenfeld and Haeckel. A further reference may here be made to a paper by R. Baar (1903). He had a specimen "from Honolulu" that he identified (p. 30) as *Stelospongia lordii* Lendenfeld. Lendenfeld's species was a sponge from the Red Sea, and was described so vaguely that it might be a *Dysidea* or an *Ircinia*, or probably a *Polyfibrospongia*, but not even its generic allocation is clear. Baar's specimen was a macerated fragment that had lost all the significant bases for its identification. From his description one cannot even be sure to what family it belonged.

A bit of philosophy is indicated. Many sponge specimens are found in sea or on shore that cannot be identified. Often the sponge skeleton coheres for months after death, losing its characteristics bit by bit. Pathologic as well as moribund sponges get collected. Beach-worn skeletons flourish in museums. The author has been urged by museum authorities to identify EVERY specimen, when sound judgment indicated otherwise. Both Lendenfeld's and Baar's specimens above mentioned should have been frankly reported as unidentifiable, thus sparing the printer and reader alike.

DESCRIPTIONS OF SPECIES

Haliclona flabellodigitata Burton

The sponge thus identified was dredged 19 February 1948 from a depth of fifty meters, three kilometers south of Pearl Harbor. It was semi-incrusting, with convoluted lobes that were about 1 mm. thick. The entire sponge was not much more than 1 mm. thick, and covered an area about 1 cm. square. The color in life was whitish orange and the consistency was soft. The surface was not hispid, and (as is common in small sponges) no pores nor oscules were evident. There is no ectosomal specialization. The flagellate chambers are scattered, and generally about 35 microns in diameter. The skeleton comprises a few spic-

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ular tracts or fibers, with little spongin, only two to four spicules per cross section. The spicules are chiefly oxeas 2.5 to 3 by 160 microns. There are also numerous thinner spicules, 0.5 × 120 microns; these may be termed raphides, but on the other hand, may merely be juvenile forms of the larger spicules.

FIG. 1. Camera lucida drawing (× 635) of a typical spicule of the sponge identified as *Haliclona flabellodigitata*.

Burton (1934: 534) described *Haliclona flabellodigitatus* from northeastern Australia. His specimens, and that now under discussion, are notable within the large genus *Haliclona* for the relative thinness or slenderness of their oxeas. All *Haliclonas* are much like one another, and the question of "what is a species?" is even more perplexing in regard to this genus than for other genera. Spongologists are confident that many species of *Haliclona* exist, but for lack of striking characteristics have paid attention to small differences. It is far from certain that this Hawaiian sponge is conspecific with that described by Burton, but there is significant resemblance. It seems regrettable to add more and more new names in so crowded a genus, and therefore this tentative identification is made.

Xytopsues zukerani new species

This new name is based upon a single specimen, to be deposited in the U. S. National Museum, collected 14 February 1948 by dredging south of Diamond Head (Honolulu), at a depth of 75 meters. It was a small amorphous sponge, less than 1 cm. thick, less than 5 cm. in diameter. The color in life was orange, and the consistency of the soft sponge was obscured by its content of debris. There was no conspicuous dermal specialization, and the pores and oscules were closed,

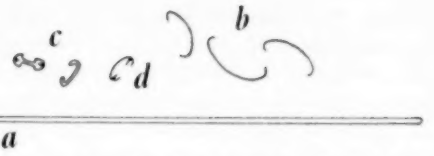

FIG. 2. Camera lucida drawing (× 635) of spicules of *Zytopsues zukerani*: *a*, Strongyle; *b*, sigmas; *c*, typical chela (arcuate) front and side views; *d*, a typical chela (unguiferate).

not evident. The sponge tissues held the mass together, but were otherwise confined to the interstices of a large quantity of calcareous sand. Some obviously foreign spicules were present, and in such cases as this it is always difficult (or impossible) to be sure which spicules are proper. The abundant, widely distributed ones are, however, probably proper. These include straight smooth strongyles 1.5 by 190 to 3 by 220 microns, contort sigmas 22 to 26 microns in chord length, and isochelas 12 microns long. The latter generally lie on one side in spicule preparations, as do palmate chelas that have narrow shovels. One isochela was found to be unguiferate, as illustrated in Figure 3*d*, but more seem to be arcuate, verging upon palmate, as shown in Figure 3*c*.

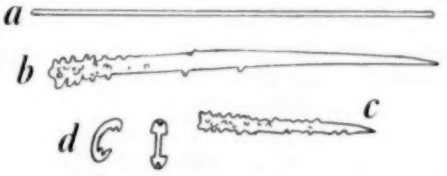

FIG. 3. Camera lucida drawing (× 635) of spicules of the sponge identified as *Lissodendoryx calypta*: *a*, Tornote; *b*, acanthostyle; *c*, echinating acanthostyle; *d*, arcuate isochela, side and front views.

The type of the genus *Xytopsues* was described as *Phoriospongia osburnensis* by George and Wilson (1919: 154) and transferred to *Xytopsues* by de Laubenfels (1936: 55). It was found at Beaufort, North Carolina. This western North Atlantic sponge is much like *X.*

zukerani except that its chelas have shafts that are pronouncedly curved, as in the letter "C." The other species already in *Xytopsues* was described as *Desmacidon griseus* by Schmidt (1870: 55). It is common in the West Indies and Bermuda, and is distinctive for its conspicuously unguiferate chelas. The species *zukerani* is thus characterized by its rather typically arcuate chelas and by its orange color. The name is given in recognition of the services to science of Lester Zukeran of the Hawaii Marine Laboratory.

Pellina sitiens Schmidt

The sponge thus identified was collected 29 March 1948 from a concrete dry dock at Pearl Harbor. It was out of water at the time of collection, but so placed as to be usually two or more meters under the surface. It covered an area about 5 × 7 cm. and consists mainly of oscular tubes 3 to 6 mm. in diameter; many of them attain a height of 2 cm. The walls of the tubes are paper-thin. The consistency is like that of wet paper. The surface is smooth, the pores not evident. The color in life was a pale dull yellow, the appearance well described as semi-transparent. The ectosome contained abundant spicules tangentially placed. The endosome was especially full of conspicuous flagellate chambers, round and 30 microns in diameter. The spicules are oxeas, chiefly in confused arrangements, and 15 × 450 to 12 × 480 microns in dimensions.

Ridley (1884: 414) described *Pellina eusiphona* from the Indian Ocean, and de Laubenfels (1954: 98) so identified a sponge from Ebon (Marshall Islands). The Hawaiian sponge is intermediate between that of the Western Pacific and Indian Ocean on the one hand, and the common North Atlantic species on the other hand. The latter was originally described as *Eumastia sitiens* by Schmidt (1870: 42). The Hawaiian specimen agrees in color with *sitiens*, and not with *eusiphona*, and it is possible that *eusiphona* should fall in synonymy with *sitiens*, although this step is not taken here. Another possibility, also rejected, but with misgivings, is that a new name might be needed for the Hawaiian *Pellina*.

Myxilla rosacea (Lieberkühn) Schmidt

This species has been reported from Kaneohe Bay (de Laubenfels, 1950: 17). The Hawaiian specimens there recorded were orange-red. On January 19, 1948 some others were found in Oahu with the clear red color that is characteristic of *Myxilla rosacea* elsewhere in the world.

Lissodendoryx calypta de Laubenfels

The sponge thus identified was dredged 14 February 1948 south of Diamond Head (Honolulu), Oahu, at a depth of about 30 meters. It was a thin incrustation, less than 1 mm. thick, of a rich carmine red color. The consistency was mediocre, the surface smooth, with no pores and oscules that could be certainly identified. The skeleton consists of spicules in confusion. There are straight smooth tornotes that may be regarded as ectosomal, 2 × 165 to 2.5 × 200 microns. The principal megascleres are acanthostyles 6×60 to 9×160 microns in dimensions. The smaller ones are spined throughout their entire length. The larger ones are smooth from the pointed end nearly halfway to the blunt end. The certain microscleres consist only of abundant isochelas of typical arcuate shape. Some extremely thin straight spicules may be raphides, but may more likely be juvenile tornotes.

Lissodendoryx calypta was described by de Laubenfels (1954*b*: 133) for a specimen from Eniwetok. It had smaller isochelas in addition to many like those in the Hawaiian specimen, and it lacked the larger acanthostyles, but the two agree in their lack of sigmas, lack of smooth styles, and thinness of incrustation.

Axechina lissa new species

This new name is based upon a single specimen, to be deposited in the U. S. Na-

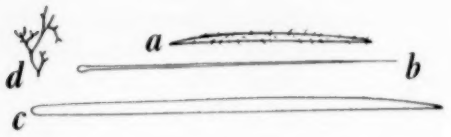

FIG. 4. Camera lucida drawing (× 635) of spicules of *Axechina lissa*: *a*, Microspined oxea; *b*, tylostyle; *c*, style; *d*, freehand sketch of the sponge × 0.3.

tional Museum, dredged 14 February 1948, near Koko Head, Oahu. It is ramose, with cylindrical dendritic branches 3 mm. in diameter, reaching a height of 7 cm. The color in life was a deep pink, which color was briefly transferred to the alcohol in which it was preserved. The surface is comparatively smooth, with no evident oscules, but with abundant pores each about 100 microns diameter, about 25 pores per square millimeter. There is a fleshy dermis about 20 microns thick. The spherical flagellate chambers are 25 to 30 microns in diameter. The endosome contains a reticulation of keratose fibers 12 to 30 microns in diameter, most commonly about 15 microns diameter. The smaller ones are cored by a single row of spicules, the large ones by as many as three spicules per cross section. The mesh of the reticulation is 50 to 100 microns in diameter, most often about 65 microns. The reticulation forms an axial core to the branches, about 1 mm. in diameter, but whereas it is generally a rather dense core, in places it opens to form a central hollow as much as 0.7 mm. diameter.

The spicules which lie in, or "core," the fibers are microspined oxeas, about 4 to 90 microns in dimensions. There are many smooth styles perpendicular both to the axial specialization and to the surface of the sponge, in plumose fashion, points out. These range from 6 × 185 microns as illustrated, up to 7 × 270 microns. There are also present thin tylostyles, often parallel to the axial specialization, their points towards the apices of the branches. These are typically 1 × 135 to 1.5 × 160 microns in dimensions.

This is the second species for the genus *Axechina*, which was established by Hentschel (1912: 417) for the species *raspailioides* from the East Indies. That and the present species agree in the raspailoid habitus, with an axial specialization of fibers cored with acanthoxeas, surrounded by radially placed smooth styles. Hentschel's species also had thin styles as long as 2200 microns, whereas the present sponge has instead the much smaller tylostyles. The East Indian sponge was strongly hispid, whereas the Hawaiian one is comparatively smooth; the specific name that is applied here is based on the Greek word for "smooth."

Eurypon distincta (Thiele) de Laubenfels

Sponges thus dubiously identified were dredged 14 February 1948 south of Diamond Head (Honolulu) at a depth of 75 meters, and 19 February 1948 south of Pearl Harbor, depth 50 meters. These were lipostomous crusts 100 to 300 microns thick, comparatively smooth, but microscopically hispid. This latter character results from a series of smooth tylostyles which generally are erect upon the substratum, points up. These spicules range from 10 to (generally) 17 microns thick, by 1000 or more microns long. Among them are numerous acanthostyles 6 × 75 to 8 × 60 microns in dimensions.

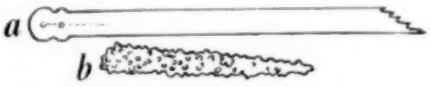

FIG. 5. Camera lucida drawing (× 635) of spicules of the sponge identified as *Eurypon distincta*: *a*, Head portion only of a tylostyle, showing the double-headed condition that frequently occurred in Hawaiian specimens thus identified; *b*, acanthostyle.

These specimens were a lovely blue in life, but after preservation the color faded and the sponges could not be found on the masses of coralline material upon which they grew. It had been intended to describe them as a new species, based on the color, but this now seems inappropriate.

Thiele (1903: 956) described a sponge as *Hymeraphia distincta* from the East Indies. This was transferred to *Eurypon* by de Laubenfels (1936: 110). Thiele does not cite the color in life, but the spicules of his *distincta* are similar to those of the Hawaiian sponges now being discussed.

There is a sound criticism for the dubious identification that is here made: it tends to indicate a faunal relationship between Hawaii and the East Indies that is not certainly valid. It is more likely that the vivid blue Hawaiian *Eurypon* specimens really do represent a distinctive species.

Microciona haematodes new species

This species was dredged 10 April 1949 near Kaena Point, Oahu, at a depth of more than 200 meters. It was growing on other sponges, of the genera *Stellettinopsis* and *Dorypleres* (q.v.). Quite likely it also grew on other substrates in the vicinity, but was not picked up by the dredge except on the more massive sponges. It was a persistently thin crust much less than a millimeter thick but spreading laterally indefinitely. A number of patches were visible, each about as large as a postage

FIG. 6. Camera lucida drawing (× 635) of spicules of *Microciona haematodes*: *a*, Tylostyle; *b*, style; *c*, acanthostyle; *d*, isochela; *e*, toxa, perhaps foreign.

stamp, and nearly as thin. They were conspicuous because of their blood-red color. The name proposed here is derived from the Greek, meaning "blood stained." The specimens are to be deposited in the U. S. National Museum.

As is characteristic of such thin sponges, little can be said as to consistency, oscules, and pores. The skeleton is completely consistent with placement in the genus *Microciona*, and yet is remarkable. Typical members of this genus have a principal skeleton of smooth styles or subtylostyles arranged as fibers or tracts. The present species does contain a few, but only a few smooth styles, scattered and secondary. Typical *Microciona* has the tracts or fibers echinated by acanthostyles, which are generally scanty in numbers, even to the point of being difficult to find. The present species instead has principally acanthostyles of the echinating sort.

Comparison with the genus *Myxilla* is interesting. In that genus the spicules that apparently should be principal are rare, and the spiny echinating spicules abound. In *Myxilla* and in *haematodes* these acanthostyles form a distinctive isodictyal reticulation with many parallel spicules on each side of the triangular or polygonal meshes. This has been compared to a number of rooms built "log-cabin" style. In *Myxilla*, however, the dermal spicules are diactinal, whereas *haematodes* has monactinal ectospicules as in *Microciona*. The present species has palmate isochelas as typical of *Microciona*, but astonishingly almost or quite lacks the toxas that are present in nearly all species of *Microciona;* one was found, but was not certainly proper. Spicule dimensions are as follows: dermal tylostyles 2 × 200 to 4 × 400, generally 3 × 300 microns; smooth styles of the "coring" type 8 × 270 microns; acanthostyles 6 × 80 to 6 × 100 microns; palmate isochelas 15 microns long.

Microciona maunaloa de Laubenfels

This species has been reported (de Laubenfels 1951: 260) as occurring around the Island of Hawaii. A rather typical specimen was collected in Oahu 27 September 1947 in Waialua Bay at a depth between 4 and 8 meters. A *Microciona* collected 19 February 1948 south of Pearl Harbor may have been this species, but its toxas (?) were only once-bent instead of being the usual thrice-bent shape.

Ulosa rhoda new species

The type of this species was dredged 19 February 1948 at a depth of 50 meters, 3 kilometers south of Pearl Harbor. Another specimen was dredged 14 February 1948 at a depth of 20 meters, south of Diamond Head (Honolulu). The shape is cylindrical with, in each case, a single short branch. The diameter is about 2 cm. and the height about 8 cm. The consistency is spongy. The surface is coarsely cavernous, thus obscuring the pore-oscular situation. The caverns are about 1 mm. in diameter, representing the mesh of a fibro-reticulation of which the fiber ends often protrude from the surface. These fibers are 50 to 150 microns in diameter and contain many of the spicules, but there are also numerous spicules loose between the fibers. The spicules are all styles, varying generally from 13 × 400 to 15 × 310 microns; a few smaller ones are doubtless juveniles.

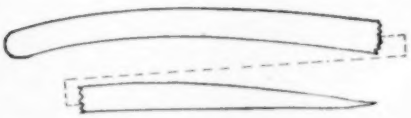

FIG. 7. Camera lucida drawing (× 635) of a typical spicule (Style) of *Ulosa rhoda*.

These sponges were particularly striking red in color when alive, and the name selected is based upon a Greek word for "rose." So far as is known, this color is unique in the genus.

Axinella solenoeides new species

This species was dredged 10 April 1949 at a depth of more than 200 meters, near Kaena Point. The specimens are to be deposited in the U. S. National Museum. It is a ramose sponge, with cylindrical branches 2 to 3 mm. in diameter, and up to 6 cm. high. The color in life was light red and the consistency flexible. The surface had the smoothness of velvet, and was lipostomous. As is typical of the genus *Axinella*, there is an axial specialization

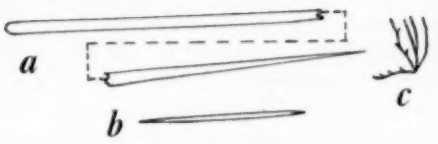

FIG. 8. Camera lucida drawing (× 635) of spicules of *Axinella solenoeides*: *a*, Style; *b*, oxea (Microxea); *c*, freehand sketch of the entire sponge, × 0.3.

comprising diactinal spicules, surrounded by outward-pointing monaxons. The axial specialization is generally a relatively solid core of fiber and spicule, and in places this is true of *solenoeides*, but in many places this sponge has an axial specialization that is a tube, with fibers and oxeote spicules around the hollow and parallel to it. The specific name is derived from a Greek word meaning "hollow," the distinctive characteristic of this new species. The oxeas vary from 1 × 60 to 3 × 90 microns; the styles of the plumose outer portion also vary considerably but are often about 4 × 160 microns in dimensions. The smaller oxeas may even constitute a category of raphides.

Homaxinella anamesa new species

This species was dredged 10 April 1949 at a depth of more than 200 meters, near Kaena Point. There were two separate collections; the type specimen is pronouncedly ramose with cylindrical branches 8 to 14, generally 10 mm. diameter. It reaches a height of 13 cm.

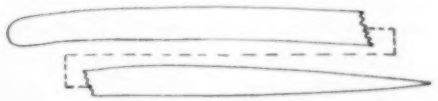

FIG. 9. Camera lucida drawing (× 635) of a typical spicule (Style) of *Homaxinella anamesa*.

The second specimen is somewhat flabellate due to lateral fusion of branches and is only about 7 cm. high. The color in life was bright vermillion red and the consistency spongy but easily torn. There was some obvious slime

production. The surface is conulose, with conules 1 mm. high and 2 to 3 mm. apart; between them are numerous apertures upwards of 1 mm. diameter and only 2 or 3 mm. apart on centers. Exhalant openings are not obviously differentiated from the inhalant ones. The skeleton consists of plumose tracts or fibers profusely echinated by smooth styles. This and the whole external appearance strongly resembles the *Homaxinella* (species *rudis*) that is so abundant in the Bermudas. That has styles 9 × 280 to 11 × 320 whereas the Hawaiian *Homaxinella* has styles 12 × 240 to 16 × 320 microns. The oscules are conspicuous in *rudis*. The other *Homaxinella* with the striking appearance of *rudis* and *anamesa* is *trachys* de Laubenfels (1954: 171) from Ebon, but its styles were much larger, 16×550 microns. The name *anamesa* is derived from a Greek adjective signifying "intermediate" or "in between." The specimens are to be deposited in the U. S. National Museum.

Densa distincta new species

This species was dredged 19 February 1948 at a depth of 50 meters, 3 kilometers south of Pearl Harbor. The specimen is to be deposited in the U. S. National Museum. It is an irregular mass, almost lobate, with projections about 3 or 4 mm. thick. The whole sponge is about 3 cm. diameter. The color in life was bright orange and the consistency dense, like cheese. The surface is smooth and lipostomous. The sponge is full of spicules in utter confusion. The majority are oxeas, but many are strongyles. The sizes range from 3 × 600 to 6 × 600 microns.

FIG. 10. Camera lucida drawing (× 635) of spicules of *Densa distincta*: *a*, A typical one of the oxeas, shown complete, but in three sections; *b*, the ends only of one of the strongyles, the long middle portion not shown.

This sponge answers to the definition of *Densa*, which is to say, *Hymeniacidon*-like, but with diactinal instead of monactinal spicules, but this is a heterogenous genus. The type, *Densa araminta* de Laubenfels (1934: 14), is a cavernous sponge with spicules of more commonplace proportions, whereas those of *distincta* are extraordinarily thin in proportion to their length. The other species that has been referred to this genus is *Densa mollis* de Laubenfels (1954: 191). It had small spicules and verged toward the genus *Collocalypta* by reason of mucous content, but *Collocalypta* has spongin fibers. Here is a genus of three species so diversified that their close relationship is questionable, yet they scarcely warrant erection of more new genera. The genus *Hymeniacidon*, which matches *Densa*, is similarly diversified and possibly polyphyletic.

Anthosigmella valentis new species

This species was dredged 10 April 1949 from a depth of more than 200 meters near Kaena Point. The specimen is to be deposited in the U. S. National Museum. It was a massive, rounded sponge, 2 × 5 × 9 cm. in size, dark drab in color, cartilaginous in consistency but packed with coarse calcareous sand. The oscules and pores appear to have closed. The surface is smooth, the interior finely cavernous, and (as noted above) full of debris. The skeleton comprises stout smooth tylostyles 7 × 300 to 9 × 425 microns in dimensions, and peculiar spirasters 10 to (rarely) 14 microns in chord measurement. These are essentially sigmoid microstrongyles with a single row of tuberculate processes.

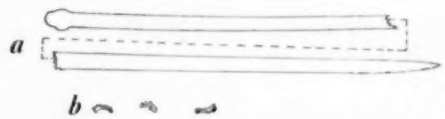

FIG. 11. Camera lucida drawing (× 635) of spicules of *Anthosigmella valentis*: *a*, Tylostyle; *b*, three of the distinctive microscleres.

There are also present microscleres that are intermediate between typical spirasters and the peculiar forms.

There are two species already in *Anthosigmella*, each widely distributed. The first was described as *Thalysias varians* by Duchassaing and Michelotti (1864: 86), and was made the type of *Anthosigmella* by Topsent (1918: 557). This sponge is abundant throughout the West Indian region. The second species was described as *Spirastrella vagabunda* by Ridley (1884: 468). It is abundant throughout the Indian Ocean, East Indies, Philippines, and the islands of the West Central Pacific. In comparison to these, *valentis* is distinctive for its extensive content of sand. In its smallness of oscule it is more like *varians* than *vagabunda*, and its microsclere shape is more like that in *varians*, but the microsclere size is even smaller than in *vagabunda*, which in turn averages smaller than in *varians*. *Valentis* is a Latin word meaning "vigorous, valiant, healthy."

Prosuberites oleteira new species

This species was collected 29 March 1948 on the Naval dry dock at Pearl Harbor. It was placed so as to be generally two or more meters below the surface, but would occasionally be out of water entirely, as at the time of collection. It occurred in at least three different places on the dock. Another specimen was dredged 14 February 1948 from 18 meters depth, south of Diamond Head (Honolulu).

This is a paper-thin sponge, of a vivid dark yellow color, verging toward orange, smooth to the naked eye, lipostomous and softly colloidal. Extensive subdermal spaces are present. The skeleton consists of tylostyles with rather flat heads, many are about 7 × 230 microns in size, but there is variation; some are nearly twice that length. There is a tendency for these spicules to be placed erect, heads at the substrate and points up and out. The flesh is so thin, however, (50 to 150 microns only) that the longer spicules merely lie in confusion.

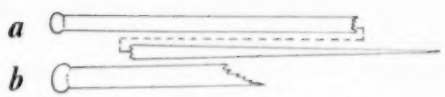

FIG. 12. Camera lucida drawing (× 635) of spicules of *Prosuberites oleteira*: *a*, Commonplace tylostyle; *b*, head only of a somewhat unusual sort that is common in this species.

The type is to be deposited in the U. S. National Museum.

The genus *Prosuberites* is a puzzling one. Burton (1934: 316) would drop all of it, and all of *Protosuberites* in synonymy to *Suberites*, assuming that the former two consist only of juvenile *Suberites*. The typical *Prosuberites*, however, has spicules far larger than those of *Suberites*, and (more important) does not have special dermal smaller tylostyles. There is good evidence that some of *Prosuberites*, like the Hawaiian sponge now being discussed, persistently remain encrusting, growing only laterally once they are established.

As for *Protosuberites*, there are only two species firmly placed therein, each established by Swarchewsky (1905: 36), and neither one satisfactorily described. Neither they nor the characters of the genus are adequately known. It is probably a synonym, perhaps of *Pseudosuberites*, but now has uncertain status.

In *Prosuberites*, there are now three names, established for Japanese sponges by Thiele (1898: 40); these are *sagamensis*, *exiguus*, and *inconspicuus*. All three are described with excessive brevity and must be regarded as ill-known. There seems to be, however, no clear reason for differentiating them from one another, and all seem to be juvenile *Suberites;* all three are here regarded as being *Suberites sagamensis*. *Alcyonium epiphytum* Lamarck (1815: 163) is also here transferred to *Suberites*, being a juvenile.

In *Prosuberites* there are now six species with relatively huge spicules. These spicules, however, differ radically in proportions from one

species to another. The six species include the type, *P. longispina*, and *P. incrustans*, *mexicensis*, *perforatus*, *rugosus*, and *sisyrnus*.

In *Prosuberites* there are now three species with smaller spicules, only a little larger than those that are typical of *Suberites*, but not differentiated into categories as are those of *Suberites*. These three are *brevispinus*, *epiphytoides*, and *brondstedi*. To them should be added the similar species described as *Hymeraphia spinularia* by Bowerbank (1875: 282). *Protosuberites brevispinus* was described by de Laubenfels (1951: 215), but the author had no opportunity to correct proof. Thus it happened that by accident the spicule size was omitted from the original publication: it was 6 × 520 to 6 × 550 microns.

Prosuberites oleteira has spicules a little larger than those of the four species that are discussed in the preceding paragraph, but much smaller than the spicules of the more typical six. It has a lethal effect which is not recorded for any of the others, and which may be unique. On the other hand, this characteristic may be present in one or more of the *brevispinus* type, in which case some synonymization might later be in order.

It was clear that *oleteira* was destroying other sessile forms as it spread its thin growth outward. Some encrusting sponges grow into interstices, or are left in interstices; these latter spaces are angular, with rounded protrusions entering them. The growth of *oleteira* instead made rounded lethal encroachments over its neighbors, which were chiefly ascidians and annelids of the type that form small calcareous tubes. The name *oleteira* is derived from a Greek word meaning "murderess."

Stellettinopsis kaena new species

This species was dredged 10 April 1949 near Kaena Point, from a depth of more than 200 meters. Two separate specimens were collected, both to be deposited in the U. S. National Museum. Each is an irregular mass.

FIG. 13. Camera lucida drawing (× 635) of spicules of *Stellettinopsis kaena*: *a*, Central portion only of one of the oxeas to show its relative size; *b*, two of the sceptrelliform streptasters; *c*, two of the oxyeuasters.

That which is selected as type was 6 × 9 × 11 cm.; the other was 11 × 14 × 27 cm. The former was drab, darker at the surface than inside. The latter was so dark as to be nearly black. The consistency is cartilaginous and the surface is rough and lumpy. Both specimens contain foreign matter in scattered places, as though they had grown over neighboring organisms; this is not a case of incorporating foreign debris in proper skeletal structures. Both specimens were much overgrown as well. The type is nearly covered by patches of calcareous algae, the other specimen by a thin crust of *Microciona haematodes*. Both specimens are densely packed with large oxeas in confusion. These are somewhat larger in the type, ranging up to 36 × 2400 and 42 × 2000 microns in dimensions. In the other specimen sizes around 14 × 1000 microns are common. The microscleres include oxyeuasters 16 to (rarely) 20 microns in diameter, and streptasters uniformly about 12 microns in length. These show a pronounced tendency to have many spines arranged in two nodes that divide the spicule into equal thirds of length, no spines elsewhere except sometimes a few spines at the extreme ends.

Carter (1879: 349) described *Stellettinopsis simplex* from Australia. It has the sceptrelliform streptasters as in *kaena*, but they are 17 microns long, and are accompanied by diversified kinds of euasters. The other species which is most nearly like *kaena* was described from the Bermudas as *Stellettinopsis ketostea* (de Laubenfels, 1950: 112). The resemblance is indeed close, but *ketostea* had much larger euasters.

Dorypleres pleopora new species

The type of this species was dredged 19 February 1948 at a depth of 50 meters, 3 kilometers south of Pearl Harbor. A second specimen was dredged 10 April 1949 from a depth of more than 200 meters, near Kaena Point. The type specimen was a thin crust, but the second specimen was massive, 10×13×16 cm. in size. Each was bright lemon yellow and each darkened noticeably, to a sort of olive green or drab, after two or three weeks of preservation in alcohol. The consistency was cartilaginous. The surface was uneven, rough, but not especially hispid. No obviously exhalant openings were evident, but especially on the type specimen there were numerous scattered conspicuous pore sieves. In them the openings were 4×50 to 50×80 microns in size, and separated by narrow partitions only 40 microns thick. The ectosome contains more asters than the endosome; the latter is

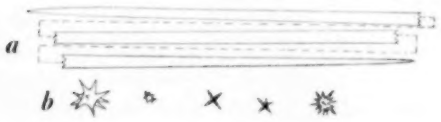

FIG. 14. Camera lucida drawing (× 635) of spicules of *Dorypleres pleopora*: *a*, One of the oxeas, shown complete, but in three sections; *b*, five of the asters.

packed with oxeas in confusion. These are 6×600, 8×600 to rarely 8×800 microns in dimensions in the type specimen, somewhat larger in the second specimen. The asters are of two distinct sorts. There are spherasters with many smooth, sharp rays, diameters 7 to 20 microns, with all intermediate sizes. There are also oxyeuasters regularly 10 microns in diameter, with few, often only 6 or 8 rays. The type is to be deposited in the U. S. National Museum.

The pore areas suggest those of the sponge described by Dendy (1916: 247) as *Aurora cribriporosa*, but that sponge had radiate symmetry and a thick cortex, two sizes of oxeas (one huge) and much larger asters. It never belonged in *Aurora*, which is a choristid genus; nevertheless *Aurora* needs attention because the name was preoccupied in 1887 by Ragonot for Lepidoptera, hence the following action is taken here:

Aurorella (new name) is here proposed for *Aurora* Sollas (1888: 187). The genotype is *Stelletta globostellata* Carter (1883: 353).

The above-mentioned *cribriporosa* has been put in *Rhabdastrella*, and so has *Diastra sterrastraea*, the genotype of *Diastra* Row (1911: 301). Because of its sterrasters, it is here proposed that *Diastra* be restored to full and valid generic standing. On the other hand, *Rhabdastrella* Thiele (1903: 934) is in no significant way different from *Dorypleres* Sollas (1888: 426), and should be dropped in synonymy to *Dorypleres*. Within this genus the other species closest to *pleopora* is *splendens* de Laubenfels (1954: 226) from Ponapé. These two species have oxeas much smaller than those of the other species of the genus, and little or no radiate structure; they conceivably might be given separate generic standing. *Dorypleres splendens* was bright orange, and its microscleres were spined; furthermore, it did not have obvious pore-sieves.

Erylus rotundus Lendenfeld

This species was dredged 19 February 1948 at a depth of 50 meters, 3 kilometers south

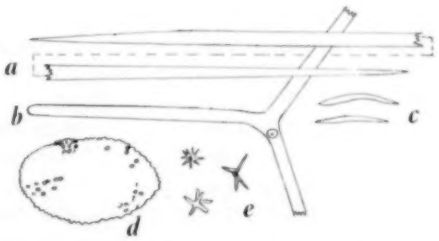

FIG. 15. Camera lucida drawing (× 635) of spicules of *Erylus rotundus*: *a*, Oxea; *b*, portion of a tetraxon spicule, only one of the four rays is shown complete, and one projects directly toward the observer; *c*, microxeas; *d*, solenaster; *e*, variations of form in tylasters.

of Pearl Harbor. There were two subspherical specimens, human fist size, nearly black exteriorly but drab as to interior. The consistency was cartilaginous. The oscules were about 1.5 mm. in diameter. The surface revealed numerous pores 70 to 140 microns in diameter. The ectosome is a cortex 100 microns and more in thickness. The endosome is vaguely radiate in architecture. The spicules are principally smooth oxeas, about 9 × 500 microns, but there are scattered tetraxons with rays about 7 × 140 microns. There are four kinds of microsclere. There are microxeas about 3 × 50 microns, often bent, indicating that they may represent large asters with rays reduced in number to two. There are microtuberculate chiasters or tylasters about 17 microns in diameter, with few rays, and others only 12 microns in diameter with many rays. Finally there are the peculiar aspidasters that characterize the genus *Erylus*. They are oval plates 3 microns thick and about 50 × 85 microns in surface size, completely covered with tubercles about 2 microns high and 2 microns in diameter. These plate-or-scale like spicules constitute a sort of dermal armour. They develop from asters, all of whose rays lie in a single plane.

In 1904 and 1905 Alexander Agassiz, aboard the U. S. Fish Commission Steamer "Albatross," collected in the Eastern Tropical Pacific. The vast numbers of sponges thus acquired are presumably in the collections of Harvard University at Cambridge, or in the U. S. National Museum. They were, almost immediately, made available for study by R. von Lendenfeld. In 1910 he published in the memoirs of the Museum of Comparative Zoology of Harvard a huge quarto volume on the family "Geodidae" (it should be Geodiidae) and another nearly as large on the family "Erylidae." In 1915 a massive two volume work appeared on the Hyalospongea thus collected. The volume on Geodiidae concerns only one certain genus, and scarcely a dozen valid species, which could be thoroughly described in 20 or 30 pages. The volume on Erylidae concerns less than half a dozen certain species, which could be appropriately described and discussed in about a dozen such large pages. The volumes in question are masterpieces of verbosity.

The scientists who travelled on the "Albatross" found no hyalosponges near Hawaii, nor any *Geodias*, but did find an *Erylus*. As was his custom, Lendenfeld made three species and two additional subspecies for it. Using his criteria, the specimen described above would be yet another species, and the next one collected in the future would be yet another. Lendenfeld used the names *rotundus*, *caliculatus*, and *sollasii;* the latter two of these names are here dropped in synonymy to *rotundus* (page 290), with some misgivings that all may possibly be synonyms of *Erylus nobilis* Thiele (1900: 48). Lendenfeld records his *Erylus caliculatus* from north of the Island of Hawaii, *Erylus sollasii* from south of Molokai, his *Erylus rotundus* from near Hawaii, and also from Hawaii and Molokai.

(?) **Leucosolenia vesicula** (Haeckel) Dendy and Row

Haeckel (1872: 41) described a remarkable sort of sponge, calling it first *Ascetta vesicula*, then later calling it *Clistolynthus vesicula*. He states that he found four specimens of it on floating Sargasso-weed, collected by Captain Halterman in the neighborhood of Honolulu. The weed was densely covered with hydroids and bryozoans. All four examples of *vesicula* were hollow balls with no trace of an oscule, total size 2 to 3 mm. in diameter. The only spicules present were sagittal triaxons with rays 10 × 80 to 12 × 90 microns in dimensions. It seems highly probable that these were immediate post-fixation stages of some sponge that may have appeared quite different when adult–this could even have been a juvenile *Leuconia* or (more likely) a *Leucetta*.

FRESHWATER SPONGES OF OAHU

In April 1941 Professor Arthur Svihla of the University of Washington sent the author

a manuscript describing freshwater sponges that he had personally found at Haepuaena on the Hawaiian Island of Maui and that Otto Degener had found on Oahu. Professor Svihla identified these as *Heteromeyenia baileyii* new subspecies. The present author concluded from the excellent descriptions rendered that they were typical *baileyii*, not a new variety. Therefore Professor Svihla so published them in a short article in SCIENCE.

Otto Degener and the present author repeatedly collected freshwater sponges on Oahu. They are common in the streams on the west or leeward side of the Koolau Mountains. These sponges look very much like *Heteromeyenia*, and closely resemble *H. baileyii* in particular. A perplexing difficulty, however, arises.

The genus *Heteromeyenia* is set off from the otherwise similar genus *Meyenia* by a difference in the special gemmule spicules. In *Meyenia* these are birotulate or amphidisc microscleres all of a single category. In *Heteromeyenia* there are similar amphidiscs, but also a second category of much longer, attenuated amphidiscs occurs among them.

The present author collected many specimens from various Oahu locations, and from each many gemmules. Numerous microscopic preparations were made, and studied for many hours. He was never able to find a single example of the second type of microscleres; every one of the specimens keyed to *Meyenia*, not to *Heteromeyenia*.

The Oahu specimens do not match any of the species that have been described in the genus *Meyenia*. They do fit perfectly the species *baileyii* of *Heteromeyenia* in every respect except the one that is used to separate that genus from *Meyenia*. The opinion is here expressed that they are indeed *baileyii*, but that those in Oahu have a most perplexing rarity of a critical characteristic. It would be interesting if the Oahu freshwater sponges were examined on successive years, and at various times per year; perhaps there is a time when the *Heteromeyenia* characteristic appears.

DISTRIBUTIONAL NOTES

Waialua Bay was studied 27 September 1947, chiefly by face-plate diving. The following sponges were found: *Spongia oceania*, *Haliclona permollis* (?), *Xytopsiphum kaneohe*, *Callyspongia diffusa* (?), *Toxadocia violacea*, *Microciona maunaloa*, *Terpios zeteki*, *Cliona vastifica*, *Zaplethes digonoxea*, and *Leucetta solida*.

On 18 October 1947 a study was made of a large, shallow, nearly enclosed area known as the West Loch of Pearl Harbor, in a part of it called Ulumoku Pond. Sponges were abundantly present. Two or three of these proved to be *Mycale cecila* but all of the many others were *Terpios zeteki*.

On 10 December 1947 an intensive study was made of the pilings in various portions of Honolulu Harbor. One interesting observation concerned the fact that where wastes from the pineapple canneries entered the harbor there were no sponges, and few other sessile invertebrates were present. The commonest animals on the pilings seemed to be: Finger-sized grey ascidians, annelids with calcareous tubes, erect bryozoa (*Bugula?*), bivalve mollusks (*Anomia* and *Ostrea?*), barnacles (*Balanus amphitrite?*), and, on nearly every piling, the sponge, *Mycale cecilia*.

On the 24th, 25th, and 26th of January 1948 an especially severe storm struck Oahu. On January 28th the beaches were studied from the southeast tip to the northwest side, for the wrack that is cast up by the waves. The only sponges found there were *Spongia oceania*. It seems to be commoner, and to grow larger, than any other Hawaiian sponge. The natives called sponges "upi," from their word for "to squeeze," also "hu'e hu'e kai," which means "foam of the sea."

On 14 February 1948 study was made both by diving and dredging near Koko Head (near Hanauma Bay). Vernon Brock, who was the most expert diver, reported that the bottom was liberally sprinkled with specimens that were obviously *Spongia oceania*. Others found included: *Xytopsues zukerani*, *Tedania ignis*,

Lissodendoryx calypta, *Axechina lissa*, *Eurypon distincta*, *Microciona maunaloa*, *Prosuberites oleteira*, *Ulosa rhoda*, and *Leucosoleonia eleanor*.

On 19 February 1948 dredging was carried on 2 to 3 kilometers south of Pearl Harbor. The following eleven sponge species were thus collected: *Hexadella pleochromata*, *Haliclona flabellodigitata*, *Tedania ignis*, *Lissodendoryx calypta*, *Eurypon distincta*, *Microciona maunaloa*, *Ulosa rhoda*, *Densa distincta*, *Dorypleres pleopora*, *Erylus rotundus*, and *Leucetta solida*.

This is an astonishingly great variety of Porifera to be found in such a limited area with but the one method of collecting.

On 11 March 1948 a study was made of barges that had been in Pearl Harbor for three years continuously, but on that day were finally put in dry dock for cleansing of their extremely foul bottoms. A barge that had been long at Kwajalein in the Marshall Islands, and then for three months at Pearl Harbor, was studied at the same time. The latter differed in sponge fauna from the former in having specimens of *Tethya*, and in lacking calcisponges. Six species occurred on both. This boat-bottom sponge fauna included: *Haliclona permollis* (?), *Pellina sitiens*, *Mycale cecilia*, *Prosuberites oleteira*, *Zygomycale parishii*, *Terpios zeteki*, *Tethya diploderma*, and *Leuconia kaiana*.

On 29 March 1948 another batch of ship bottoms was examined in dry dock; they revealed chiefly *Pellina*, *Mycale*, *Prosuberites*, and *Zygomycale*.

On 15 April 1948 still another batch of ship bottoms was examined in dry dock; these revealed *Mycale*, *Terpios* and *Zygomycale*.

On 10 April 1949 sponges were dredged near Kaena Point, at a depth of more than 200 meters. This collection included: *Microciona haematodes*, *Axinella solenoides*, *Homaxinella anamesa*, *Anthosigmella valentis*, *Stelletinopsis kaena*, and *Dorypleres pleopora*.

These are all new species, and the assortment is strikingly different from that of shallow water Oahu.

FAUNAL RELATIONSHIPS

The Hawaiian Islands are so isolated that, as may be expected, their shallow-water invertebrate fauna is largely endemic. This is emphatically true for the sponge fauna of Oahu, as outlined above. A minority of Hawaiian sponges show relationships to species from other parts of the world; these warrant further notice.

One Hawaiian sponge has been identified as being *Pellina sitiens*, properly a North Atlantic species. This identification is dubious, in that a new name may be needed for the Hawaiian *Pellina*, but some relationship is clearly indicated. On the other hand, *P. sitiens* may prove to be circumequatorial.

Oahu sponges have been identified with the following circumequatorial species: *Dysidea avara*, *Haliclona permollis*, *Myxilla rosacea*, *Tedania ignis*, *Zygomycale parishii*, *Cliona vastifica*, *Tethya diploderma*, *Plakortis simplex*, and *Leucetta solida*.

Five sponge species from Oahu have been identified with species that are not known to be circumequatorial, and which do occur to the west of the Hawaiian Islands. These are: *Haliclona flabellodigitata* (Australia), *Callyspongia diffusa* (Indian Ocean, East Indies, Micronesia), *Oscarella tenuis* (Australia), *Lissodendoryx calypta* (Eniwetok), and *Eurypon distincta* (East Indies).

It is worthy of notice that each of these five identifications is merely tentative and is certainly questionable. Each of the five may require a new name, indicating an endemic nature.

Five sponge species from Oahu have been identified with species that are not known to be circumequatorial, and which do occur to the east of the Hawaiian Islands. These are: *Adocia gellindra*, *Toxadocia violacea*, *Mycale cecilia*, *Terpios zeteki*, and *Leucosolenia eleanor*.

The opinion is here expressed that these identifications are more nearly certain, more dependable, than the preceding five identifications.

Ekman in his "Zoogeography of the Sea," page 19 and following, summarizes faunal relationships for the Hawaiian Islands as embodied in the literature. He had no data for the Porifera, but had ample data for most of the other great divisions of the animal kingdom. He reveals a pattern of great resemblance between the marine invertebrate faunas of Hawaii on the one hand, and those of the Asiatic-Australian-East Indian regions on the other hand. The fish faunas show this resemblance to an even greater degree. Other sources point to great resemblances between the floras of Hawaii and Asia.

Endemic species are rather more prominent in the Hawaiian sponge fauna than in faunas of other animal (and plant) groups. The few exotic sponge species show astonishingly little relationships to faunas of Asia, Australia and the East Indies. Relationship between Hawaiian sponges and those of the Pacific Coast of the Americas is not great, yet it is the most nearly worthy of attention as indicating zoogeographic affinity.

Could this American relationship be due to transport of sponges on ship bottoms? Sponges occur fairly commonly among the fouling organisms. With the possibility of transport in mind, studies were made of the bottoms of vessels in dry dock at Pearl Harbor. The results were inconclusive, but not negative. It seems clear that on a long ocean voyage most of the sponges on the ship's bottom perish, but a few might possibly survive.

TAXONOMIC NOTES

An important genus of Porifera has been known by the name of *Heteronema*, a name established by Keller (1889: 339). This name is even used in the author's 1946 monograph of the order Keratosa. It should not have been used, however, because it was preoccupied in 1841 by Dujardin for a protozoan.

The genus in question is characterized as resembling *Spongia*, but having foreign debris in the secondary fibers as well as in the primary fibers. This also was the diagnosis given by Lendenfeld (1885: 543), to his then new subgenus *Silicifibris* of the genus *Spongia*, hence this *Silicifibris* warrants attention.

The first species assigned to *Silicifibris* was the new species *galea*, here designated as the genotype. It was based on a macerated skeleton of a vase-shaped sponge, 25 cm. in diameter and height, with a sharp edged rim. This shape, and all details of the skeleton as described, match the long-established genus *Phyllospongia*.

The second species assigned to *Silicifibris* was Ridley's *Euspongia foliacea*. In a personal communication, Dr. Maurice Burton of the British Museum states that *foliacea* is a synonym of Carter's *Coscinoderma lanuginosum*, which has been transferred to *Phyllospongia*.

The third and last species assigned to *Silicifibris* was *silicata*, new, which may have been a *Dysidea*. The subgenus (or genus) *Silicifibris* should be regarded as a synonym of *Phyllospongia*. A new name is therefore required for the genus *Heteronema* as above described: ***Inodes,*** new name for *Heteronema* Keller (1889: 339).

Genotype: *Heteronema erecta* Keller 1889, page 339. Sponges of the family Spongiidae, with all the fibers, both primary and secondary, containing much foreign debris. The name is based on a Greek word meaning "fibrous."

Two other similar corrections require attention. In a paper by de Laubenfels (1955) the generic names *Walcottella* and *Waagenella* are established. The first of these was preoccupied by Ulrich and Bassler in 1931, for a crustacean. The second was preoccupied by Koninck in 1883, for a mollusk. New names are therefore required, as follows: ***Walcottium*** new name for *Walcottella* de Laubenfels (1955: 82). Genotype *Scyphia pertusa* Goldfuss 1833. ***Waagenium*** new name for *Waagenella* de Laubenfels (1955: 102). Genotype *Steinmannia salinaria* Waagen and Wentzel (1888: 979).

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